The Framework Species Approach to forest restoration: using functional traits as predictors of species performance.

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by

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Abstract

Due to forest degradation and loss, the use of ecological restoration techniques has become of particular interest in recent years. One such method is the Framework Species Approach (FSA), which was developed in Queensland, Australia. The Framework Species Approach involves a single planting (approximately 30 species) of both early and late successional species. Species planted must survive in the harsh conditions of an open site as well as fulfilling the functions of; (a) fast growth of a broad dense canopy to shade out weeds and reduce the chance of forest fire, (b) early production of flowers or fleshy fruits to attract seed dispersers and kick start animal-mediated seed distribution to the degraded site.

The Framework Species Approach has recently been used as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand by the Forest Restoration Research Unit (FORRU) of Chiang Mai University. FORRU have undertaken a number of trials on species performance in the nursery and the field to select appropriate species. However, this has been time-consuming and labour-intensive. It has been suggested that the need for such trials may be reduced by the pre-selection of species using their functional traits as predictors of future performance.

Here, seed, leaf and wood functional traits were analysed against predictions from ecological models such as the CSR Triangle and the pioneer concept to assess the extent to which such models described the ecological strategies exhibited by woody species in the seasonally-dry tropical forests of northern Thailand. It was found that seed storage behaviour (orthodox and recalcitrant) was strongly linked to other functional traits and that this was the basis of observed differences in performance based on seed size. There was evidence for the existence of a leaf economic spectrum in these forests and for differing positions of deciduous and evergreen species on this spectrum. It was further found that wood hydraulic capacity and safety was more strongly linked to leaf traits than wood mechanical strength; reflecting the importance of the seasonal drought in this type of forest.

Selected functional traits were then used to predict the performance of species within the FORRU project. It was found that a combination of wood and leaf traits that encompassed mechanical strength, hydraulic capacity and water storage best described species growth rates in most years and that survival may be linked to a combination of both drought and pathogen load that differs by year due to environmental conditions.

In conclusion, functional traits were found to be valuable indicators of performance in forest restoration projects.

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Contents

1.1. Introduction

1.1. Global forests

1.1.1. Deforestation

It is well established that global forest loss is a major concern; contributing to habitat and biodiversity loss as well as global warming, loss of forest products (such as timber), soil erosion and problems with water catchment (Lamb, Erskine & Parrotta 2005).

It is estimated that 31% of world land cover is currently forest and that this has reduced by 3.2% over the last 20 years (135 million ha), a significant slowing of forest loss (FAO 2010). Although at first sight, these figures are reassuring, forest loss varies considerably by region, with some areas, such as South America losing significant amounts of forest (82.1 million ha) and others such as East Asia gaining forest coverage (45.4 million ha) (Table 1.1). Also, the broad FAO definition of forest and the very variable nature of the forested land that make up these figures are not as encouraging.

Table 1.1: Global forest coverage and deforestation data by geographical region from 1990 to 2010 (FAO 2010). Figures discussed in text are marked in bold. NA indicates figure not applicable

Country/area	Land area (10 000 ha)	Forest area (10 000 ha) % of total land mass given in brackets			Forest area lost (Negative numbers indicate gain)	
		1990	2000	2010	10 000 ha	%
Eastern and Southern Africa	99980	30431 (30)	28590 (29)	26751 (27)	3679	12
Northern Africa	94110	8512 (9)	7922 (8)	7881 (8)	630	7
Western and Central Africa	103309	35980 (35)	34343 (33)	32808 (32)	3171	9
East Asia	115754	20919 (18)	22681 (20)	25462 (22)	**-4542**	**-22**
South and South-east Asia	84741	32542 (38)	30114 (36)	29437 (35)	3105	10
Western and Central Asia	108645	4148 (4)	4220 (4)	4351 (4)	-202	-5
Europe	221472	98947 (45)	99823 (45)	100500 (45)	-1553	-2
Caribbean	2289	590 (26)	643 (28)	693 (30)	-103	-17
Central America	5107	2571 (50)	2198 (43)	1949 (38)	621	24
North America	206100	67676 (33)	67708 (33)	67896 (33)	-219	0
North and Central America	213497	70838 (33)	70549 (33)	70539 (33)	299	0
Oceania	84909	19874 (23)	19838 (23)	19138 (23)	736	4
South America	174629	94645 (54)	90432 (52)	86435 (49)	**8210**	**9**
World	1301050	416839	408516	403306	13533	NA

These FAO figures (FAO 2010) identify forest as any area where there are trees taller than 5m covering more than 10% of the area on land not used for agriculture (Table 1.1). This broad definition may, therefore, include anything from pristine primary forest through to mono-culture rubber wood plantations or severely-degraded natural forest. Further comparison of the FAO data from 2010 shows that the forest gains within East Asia are primarily due to afforestation in China. Within the time period, 34.7 million ha forest was planted and 27.5 million ha was allowed to naturally regenerate, primarily for ecological protection purposes (soil erosion and water catchment). The losses in Central and South America however, consisted of the loss of significant areas of primary forest (at least 61572 thousand ha). The figure may be much greater but cannot be proved due to limitations in individual country reporting. In many areas of the world, primary forest consists of less than 5% forest coverage. It was estimated in 2000 that 60% of the world's forests were degraded primary or secondary forest (ITTO 2002); reforested areas currently account for 7% of global forest cover (**FAO** 2010).

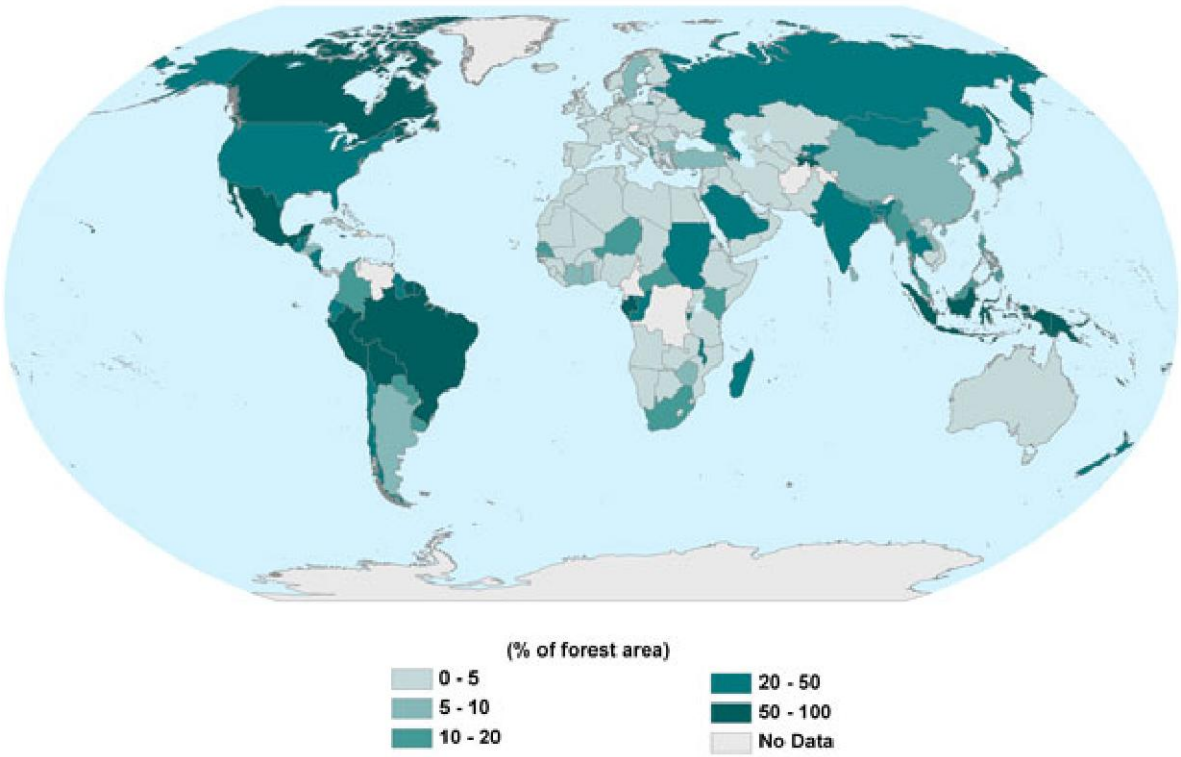


Figure 1.1: Global primary forest cover(%)by country as reported in 2010 to the Food and Agricultural organisation of the United Nations (FAO 2010)

1.1.2. Reforestation

Whilst preservation of existing pristine forest is vital, it has become increasingly clear that in some areas, too much has been destroyed to support a full range of species and habitats. It is accepted that secondary forest and planted forest must therefore play a significant role in preserving both biodiversity and ecosystem function (Lamb 2011). This is reflected in the three conventions arising from the Rio Earth Summit in 1992, which have been ratified by over 190 State and are the primary international agreements on forest ecosystems.

The Convention to Combat Desertification (UNCCD, 1994) focuses on the rehabilitation of land and the conservation and sustainable management of land and water resources. The Kyoto agreement on climate change is not primarily concerned biodiversity but does allow countries to partially offset their carbon dioxide emissions through afforestation, reforestation and re-vegetation. The Convention on Biological Diversity however, contains a commitment to the rehabilitation and restoration of degraded ecosystems, which would suggest a more robust ecological restoration approach. In addition to these Conventions, the UN Forum on Forests (UNFF) and the Intergovernmental Panel on Forests (IPF) have been created and have adopted a suite of proposals regarding the rehabilitation and restoration of degraded lands, and the promotion of natural and planted forests (www.un.org/esa/forests/about-history.html, accessed 2013).

1.1.3. What is reforestation?

Whilst there is an international commitment to reforestation, provision of forest cover actually covers a variety of different practices for different purposes. Whilst there is still some debate on the terminology used to describe human-created forests (Carle & Holmgren 2003), here, for the sake of clarity, Lamb's (2011) definitions (described below) will be used;

(a) Monoculture Plantations

Monoculture plantations consist of a single planting of a single species of tree that is raised and harvested before the planting of the next crop. Production plantation forests are essentially wood farms and may support a limited number of natural processes and functions compared to natural forest. However, plantations will support more wildlife than degraded land and some researchers have found that biodiversity may be maximised through planting indigenous tree species (Pejchar, Holl & Lockwood 2005; Carnus *et al.* 2006) and mixed species (Michelsen *et al.* 1996; Hartley 2002).

Increasingly, protection plantations (also known as reclamation planting), defined as ""forest of native or introduced species, established through planting or seeding mainly for provision of services" are being planted, primarily for the protection of water and soil services (STCP 2009). However, they may also play a role in rehabilitating land;

- Planting species adapted to degraded soils can help to restore degrade soils through nitrogen fixation and the creation of leaf litter (Parrotta 1992).

- Plantations may reduce edge effects of adjoining forest fragments (Denyer, Burns & Ogden 2006).

- Plantations may create wildlife corridors between forest fragments, thus allowing seed dispersal (Carnus *et al.* 2006).

- Plantations can facilitate succession by shading weeds and providing microclimates that allow the growth of later successional species (Carnevale & Montagnini 2002; Carnus *et al.* 2006).

(b) Rehabilitation

Rehabilitation is used to restore ecological services such as soil and watershed protection and social functions, such as the creation of parks etc. Rehabilitation usually involves the planting of some, though not all, of the species originally occurring on the site. Management, through additional plantings may be required to maintain forest cover. However, many ecological processes may be recovered and the forest may become self-sustaining, although the plant community will probably be less rich and the biodiversity far lower than that of natural forest.

Rehabilitation forests tend to have lower biodiversity value than natural forests but higher than monoculture plantations and supply all of the services (such as the reduction of edge effects, facilitation of succession, provision of wildlife corridors and restoration of soils) described for monoculture plantations.

(c) Ecological restoration

Ecological restoration (also known as forest restoration, (Elliott *et al.* 2003) aims is to restore the functionality of a natural forest, support as wide a range of biodiversity as possible and create a self sustaining ecosystem that requires minimal if any management. Whilst ecological restoration cannot hope to replicate the vegetation community of original forest, it aims to restore functionality to such a point that natural processes may then continue to repair and restore the forest over time (Elliott *et al.* 2003; Lamb 2011).

1.1.4. Why is ecological restoration necessary?

Succession is a natural process through which an ecosystem community develops on a new site or after disturbance. The classical theory (Clements 1936) suggests that an area is initially colonised by “pioneer” species which are specially adapted to the conditions found on open land. These pioneers are later replaced with other species, through a through a series of predictable stages until the final “climax” vegetation type is reached. However; the more recent “disturbance/recovery”

model (Hartshorn & Whitmore 1999) suggests mature tropical forest does not consist solely of climax vegetation, but of a mosaic of different successional stages in a constant state of flux (Chazdon 2003). Given that such succession occurs within natural forest, it is perhaps surprising that degraded forest cannot simply be left undisturbed to recover from logging or clearing for agriculture. However, whilst forest gaps formed by natural disturbances such as forest fires and tree falls are usually filled relatively quickly, the pattern of land clearance through logging or for agriculture may be characterised by features (such as spatial extent, intensity and frequency) that inhibit successional sequences (Parrotta 1992; Parrotta 1993; Turner *et al.* 1998) and are discussed more fully below.

Ecological succession is divided broadly into two categories; primary succession and secondary succession (Chazdon 2003). Secondary succession occurs where forest "residuals" remain in an area post-disturbance. These propagules may consist of seeds in the seed-bank, rhizomes, bulbs or tree stumps. The number of residuals in an area will depend largely on the intensity of a disturbance and the length of time over which the disturbance occurred (Turner *et al.* 1998). For example, wholesale clearance for 20 years may leave virtually no residuals, whereas a tree-fall event or forest fire will leave many. If propagules remain, within weeks, pioneers appear from the seed-bank, whilst late-successional species coppice from remaining stumps and the forest quickly regenerates (Turner *et al.* 1998; Whitmore & Burslem 1998).

In contrast, primary succession is succession that starts from an entirely blank slate, where there are no remnants or residuals. Primary succession may occur after a catastrophic disturbance such as a landslide, or where a forest is expanding into an entirely new area. This can be a slow process taking hundreds of years (Guariguata & Ostertag 2001). Primary succession may even be prevented from occurring at all, leaving areas at an early successional stage. Barriers to succession include a lack of seed rain the cleared area and the presence of weeds;

(a) Seed availability

The seeds of late-successional species tend to be large and animal-dispersed (Leishman & Westoby 1994). Whilst small forest gaps may be crossed by seed-dispersing animals, large areas of cleared forest do not attract them and the seeds they carry. Even if the canopy has been closed by pioneers, their small wind-dispersed seeds offer little to attract seed dispersers and later succession is inhibited by the resulting lack of seed inputs (Parrotta 1992; Robinson & Handel 1993). The distance from remaining forest fragments is important; the larger a forest gap, the less likely it is that animal-dispersed seeds will reach its centre (Parrotta 1992; Robinson & Handel 1993). Instead, the gap must be closed from the outside in by many successive generations of climax tree species. Seed dispersers may also be reduced due to habitat loss and hunting. In some countries, large seed dispersing animals such as rhinoceros as well as large-gaped frugivorous birds have become extinct locally (Galetti *et al.* 2013), so preventing species with large seeds from dispersing into cleared areas (Zimmerman, Pascarella & Aide 2000). Succession may therefore be enhanced by planting seedlings of animal-dispersed tree species (Skoglund 1992; Gerhardt 1993).

(b) Unchecked annual weeds

Whilst later succession species are shade-tolerant and can survive under a canopy, they cannot compete effectively with annual weeds (Hardwick *et al.* 2004). Where large areas have been cleared and there are no residuals, annual weeds may grow unchecked for several years. Fire is the predominant form of disturbance in seasonal tropical forests (Hardwick *et al.* 2004). The dry tinder created results in larger, more common forest fires (Swaine 1992). Young seedlings are far more vulnerable to fire than older, larger seedlings (Noble 1984; Bradstock & Myerscough 1988; Fordyce *et al.* 1997) and these regular forest fires destroy them at this early stage, so preventing them from establishing themselves sufficiently to both survive fire and to provide the shade that will reduce the annual weed growth. Where these factors occur, abandoned agricultural land and logged forest may remain at an early-successional stage such as low scrub for many years.

1.1.5. Ecological restoration approaches

Where succession is inhibited or where natural processes are happening too slowly to support ecological services such as soil and water protection, ecological restoration techniques may be valuable. A variety of such methods (but by no means all) are described below. However, most restoration projects will tailor the methods or combine them to make the most appropriate use of resources.

(a) Maximum Diversity Method (Goosem & Tucker 1995; Rodrigues *et al.* 2009)

This approach aims to replicate pre-existing biodiversity by planting as many mature canopy species as possible. Intensive management (such as weeding and mulching) is then used to "nurse" these seedlings until they are big enough to shade out weeds, which may take many years. This method is particularly useful where the restoration site is isolated from forest fragments that may act as a source sites for propagules. However, it is highly labour-intensive and later plantings are often necessary for species that cannot survive the initial conditions of the site. As all species are planted by the restoration team rather than being naturally-seeded, this method may result in a forest that does not closely resemble that which would occur naturally in the area, a fact that is exacerbated by the fact that it is used most extensively in areas where there are no remaining forest fragments.

(b) Assisted or accelerated natural regeneration method (Hardwick *et al.* 2004)

This method accelerates the natural succession process by reducing limiting factors. Fires and grazing animals are strongly controlled and weed growth is countered through the application of herbicides, manual weeding and mulching. Seed distributors are encouraged through the provision of perches, nesting sites etc. (Toh, Gillespie & Lamb 1999). The successional process may be assisted by the limited planting of pioneer species. This method is mostly used to extend or develop forest corridors between existing forest and has the advantage of needing little, or no, seedling propagation (Goosem & Tucker 1995).

1.1.6. The Framework Species Approach (Goosem & Tucker 1995)

The Framework Species Approach, developed in Queensland, Australia, involves a single planting of both pioneer and mid-successional species to re-establish basic forest structure and function. Fast growing pioneer species are planted to shade out annual weeds. Later successional species, with their larger fruit and seeds, are planted to attract seed distributors (invertebrates, birds, bats and other mammals) and the seeds they carry, therefore adding diversity to the forest. It has the advantages of a single planting (i.e. low cost to implement) and aims to be self-sustaining after the first year. It relies on being near enough to forest fragments to provide the seeds necessary for later succession and good populations of seed distributors to continue the increase in species richness.

(a) Species selection

Of the 20-30 species planted, approximately 30% should be pioneers with the rest being mid-successional to climax species. Only native species appropriate to the site (e.g. forest type, elevation etc.) and within their natural range should be planted. Species are chosen using the following criteria;

Ease of germination and growth: Species selected must be easily raised under nursery conditions. Species where seeds are not available or species with low or erratic germination rates are therefore not suitable. Additionally, very slow germinating or slow growing species may not be practical due to space constraints.

Survival: A high survival rate, both in the nursery and in the field is vital for all species used in restoration projects. The seedlings will have to survive the harsh conditions of an entirely open site such as full sun, droughts and thin and depleted soil. High regenerative ability e.g. coppicing is also valuable in these harsh conditions.

Attractiveness to wildlife: The species selected must provide resources such as foliage, flowers, fruit etc. that attract a variety of both vertebrates and invertebrates. Care should be taken to ensure that the entire species assemblage provides food all year round. Species that provide vital resources during times of fruit scarcity are of particular value, even if they do not meet other criteria.

Provision of shade: Species with thicker crowns are chosen as they provide effective shade to restrict grass and weed growth. It is important that this shade is provided as quickly as possible, so fast growth over the first 2 years is also important.

Early and reliable production of resources: Species are selected that can be relied upon to produce flowers and fruit early in their lives, between 2-5 years of age and on a regular and reliable basis. Masting species are not suitable as they will be unreliable producers.

Site specific characteristics: On specific sites, other characteristics may be a useful addition, for instance in sites with very degraded soil, nitrogen fixers may be of particular value, in others, those with a particular tolerance for fire may be important. Very few species will show all of the framework species characteristics and compromises will be required. Care should be taken to look at the entire species assemblage as part of these decisions so that the assemblage as a whole performs all of the required functions.

(b) Site Preparation

Weeds should be removed, usually through the application of a herbicide, though manual weeding/mowing may be effective depending on the site. If the ground is heavily compacted, it may benefit from ploughing or “ripping” to help water penetrate the ground and help to establish a good root system. Mulch, (straw, cardboard etc.) should be applied to retain moisture, cool soil and assist nutrient cycling.

(c) Planting

Seedlings should be planted 1.5-1.8 metres apart and well mixed by species, with particular emphasis on ensuring that the pioneer seedlings are distributed evenly across the site. Seedlings should be approximately 50-60 cm tall at planting, through pioneers may benefit from being smaller (20-30 cm), especially if they have very deep roots, which become impractical in the nursery for larger seedlings.

(d) Maintenance

Fertilizer should be supplied every four weeks during the main growing season until the end of the second year. Invading weeds must be removed until pioneers provide sufficient shade to prevent their growth. The method and timing of weeding will depend hugely on the restoration site and ecosystem. Maintenance is of particular importance on the edges of plots as additional light will encourage weed growth for some time.

(d) Site specific measures

If necessary, additional measures may be introduced to counteract any deficiencies the site has, especially in attracting seed distributors. The steps taken will be dependent on the target animal and will require knowledge of their behaviour and requirements. Regular site monitoring should be used to ensure that these measures and the chosen species assemblage are effective.

The framework species approach was initially described in a report based on ten years of research and practical experience in Queensland, Australia (Goosem & Tucker 1995) where its use resulted in extensive colonisation of restored sites within 7 years after planting (Goosem & Tucker 1995; Lamb *et al.* 1997; Tucker & Murphy 1997). However, records of formal trials are limited and the applicability of the approach to sites outside of Australia was not explored.

1.1.7. The framework species approach in Thailand

The Forest Restoration Research Unit (FORRU) of Chiang Mai was established in 1994 to develop techniques to restore forest ecosystems for the conservation of biodiversity and preservation of watersheds. Initial work was on collecting basic ecological information such as species lists and leaf, flower and fruiting phenology. Germination trials were performed on 400 species of tree and propagation techniques appropriate for small and low-technology nurseries were developed.

After a visit to Queensland in 1997, it was decided that FORRU would focus on the framework species approach. Between 1998 and 2001, a project, funded by Thailand's Biodiversity Research and Training Programme was undertaken to field-test the framework species approach in the Doi Suthep-Pui National Park in northern Thailand. Details of the Doi Suthep-Pui National Park, the field site and test methodology are provided in chapter 2. The aims of these trials were to;

(a) Identify an appropriate species assemblage for northern Thai upland forests
(b) Identify the most effective, specific methods for northern Thai upland forests where only broad recommendations were found within the original description of the framework species approach. E.g. most effective weeding and fertiliser regimes.
(c) Test the applicability of specific recommendations from the framework species approach when using the approach in northern Thailand E.g. most effective spacing.

There was in each year a control plot where no planting was done but where the area was protected from fire as well as a "framework" plot where seedlings were planted approximately 1.8m apart, 100g of fertiliser and a mulch of cut weeds was applied on planting and twice during the wet season and weeding was performed every 4-6 weeks after planting during the wet season only. Weeding and fertiliser treatments were applied for two growing seasons after planting. Approximately30 species were planted in each year. In addition, a number of trial plots tested a variety of silvicultural methods (Elliott & Anusarnsunthorn 2001; Anasarnsunthorn & Elliott 2004).

1.1.8. FORRU trials (Elliott & Anusarnsunthorn 2001; Anasarnsunthorn & Elliott 2004)

In 1998, trials focused on fertiliser application, mulching and weeding.

- Four fertiliser treatments; a) 100g at planting ; b, c and d) 50g, 100g and 200g respectively at planting and two applications during the rainy season.
- Two weeding regimes; a) every 4-6 weeks in the wet season and b) every 4-6 weeks in the wet season and once at the beginning of the dry season.
- Three mulching treatments; a) no mulch, b) a mulch of cut weeds and c) a cardboard mulch of 50cm diameter covered with cut weeds.

In 1999, there were further trials on mulching and also on planting density

- Two mulching methods; a) cardboard mulch as in the 1998 trials and b) cardboard mulch as in the 1998 trials but with a 25cm diameter.
- Two planting densities; a) 1.5m apart and b) 2.3 m apart.

In 2000, pruning, as a way of reducing transplant shock and stimulating budbreak was tested. Three treatments were tested; a) early pruning, six weeks before planting, b) late pruning 1-3 days before planting and c) no pruning.

In 2001, plots were established to test the effectiveness of placing a cardboard mulch mat about 40 cm in diameter around the base of the trees.

In 2002, plots were designed to test the effects of 3 different levels of maintenance (weeding and fertiliser application 2, 3 or 4 times during rainy season) and the use of cardboard mulch mats that were replaced after the first year with a new mat.

In 2003 plots were designed to compare the effects of two different types of fertiliser (organic Pho Garuna Brand and inorganic Rabbit Brand) and two different methods of application (mixed with soil in the planting hole or applied in a ring on the soil surface about 20 cm away from the tree stem).

The treatments applied to the 2004 continued to test different fertiliser treatments, since results from the 2003 plots were unclear.

1.1.9. Results from FORRU trials -(Elliott & Anusarnsunthorn 2001; Anasarnsunthorn & Elliott 2004)

Planted plots were more effective than the control plot (which was protected from fire only) in accelerating the recruitment of naturally establishing tree seedlings and improving the species richness of the ground flora and bird species.

Results of silviricultural trials recommended planting at 1.8m apart and weeding and fertiliser application at both the time of planting and 3 times during the first rainy season at 4-6 week intervals (repeated in the second rainy season if needed). Responses of the planted trees to cardboard mulch were highly variable among species and from year to year. In dry years and where site conditions are harsh, cardboard mulch is recommended, but where conditions are more favourable cardboard mulch may not be cost-effective.

Additionally, the provision of perches and nesting sites was shown to be of value in attracting birds and wood piles in attracting invertebrates and the seed distributors which feed on them (Wydhayagarn, Elliott & Wangpakapattanawong 2009).

Later work has focused on replicating this success in other areas of Thailand including lowland areas (Wangpakapattanawong & Elliott 2008), as well as supporting the development of similar projects. This has involved expansion into both Myanmar and Cambodia in partnership with local agencies and educational establishments (FORRU Website http://www.forru.org/en/content.php?mid=50, accessed December 2013).

As has been demonstrated in Thailand, use of the framework species approach in a new geographical area usually involves significant field trials, which can be time consuming and costly. By focusing trials on species with specific ecological strategies, it may be possible to narrow these trails to species likely to perform well, thereby reducing the need for trials. As the ecological strategies of species are linked to their physical characteristics, it may be possible to infer ecological strategy, and therefore predict performance using easily measured “species functional traits”.

1.2. Functional trait analysis

Functional traits are defined as any attribute that has potential to significantly influence the establishment, survival, and fitness of a species (Reich *et al.* 2003). Each functional trait requires investment by the plant and in a world of non-infinite resources, plant attributes often "trade off" against each other (Poorter, Bongers & Bongers 2006). For example the well-established trade-off between seed size and seed number (Smith & Fretwell 1974; Jakobsson & Eriksson 2000; Henery & Westoby 2001) and the trade-off between dense and fast wood growth (Aarssen & Irwin 1991).

Suites of functional traits tend to co-occur along a single axis of variation; species with similar life strategies often occupy similar positions on a number of different trade-off axes. The position of a species along an axis strategy dimension should relate to the conditions where it is most competitive (Grime *et al.* 1997; Westoby *et al.* 2002; Ackerly 2004; Westoby & Wright 2006). A consideration of functional traits, therefore, provides insight into patterns, important trade-offs and differing strategies employed by species within a particular environment.

During recent years, analysis of functional traits has been used widely in ecology as a useful way of looking at ecological roles (Westoby & Wright 2006; Chave *et al.* 2009; Zanne & Falster 2010), plant performance (Poorter *et al.* 2008; Russo *et al.* 2010; Wright *et al.* 2010; Zanne & Falster 2010) and as the basis of functional classifications of species (Weiher *et al.* 1999). Such is the level of interest in functional traits, a number of initiatives, such as the TRY database initiative (www.try-db.org) and Traitnet (www. traitnet.ecoinformatics.org) aim to provide a hub for the collection and sharing of functional trait information for research purposes and a number of authors have called for additional work in the field, such as the standardisation of trait measurements (Weiher *et al.* 1999; Cornelissen *et al.* 2003).

1.3. Restoration of the forests of northern Thailand

1.3.1 Seasonally-dry tropical forest

The WWF defines the area of forest found in Northern Thailand, Laos and Cambodia as “Southeastern Indochina dry evergreen forests” (Classified as IM0210), (http://worldwildlife.org/ecoregions/im0210 2013- Accessed 2013). The area is within the monsoonal belt and has a pronounced dry season between November and April (Fig. 2.2b). It may therefore be referred as “monsoonal forest” (Pennington, Lavin & Oliveira-Filho 2009) and may also be characterised as seasonally-dry tropical forest (Miles *et al.* 2006).

Whilst not as well known as tropical rainforest (which receives rain all year round), seasonally-dry tropical forest (which experiences an annual drought of at least three months (Chaturvedi, Raghubanshi & Singh 2011) covers large areas of Central and South America, Africa, India, South- East Asia and Australia (Gerhardt & Hytteborn 1992). Seasonally-dry tropical forest is much more variable than rain forest, varying from low scrub to taller forests (Pennington, Lavin & Oliveira-Filho 2009).

1.3.2 Threats to seasonally-dry tropical forest

Seasonally-dry forests are more threatened and less protected than moist and wet forest (Gerhardt 1993). It has been suggested that dry tropical forests are the most threatened of all major tropical forest types (Janzen 1988). These forests are often fragmented (Pennington, Lavin & Oliveira-Filho 2009) and only a small fraction remains, due to conversion to agricultural land over many hundreds of years (Murphy & Lugo 1986; Swaine 1992). This process is still a major threat to biodiversity (Dobson, Bradshaw & Baker 1997).Two-thirds of South-eastern Indo-china dry evergreen forests have been cleared or degraded for plantations, especially in Vietnam and Thailand (Fig. 1.2, worldwildlife.org/ecoregions/im0210 - Accessed 2013). By 1990, total forest cover had fallen to 38% (13% primary, 19.8% semi-natural, 5.2% planted).

1.3.3 Protecting the forests of Thailand

In Thailand, deforestation and forest degradation are widely recognised as major threats to environmental stability, economic prosperity and social welfare, particularly amongst rural communities (Elliott *et al.* 2003). A total logging ban in 1989 slowed the loss of primary forest loss considerably. However, a loss of 1,894,000 ha of semi-natural forest, much of which has been converted to plantations, has been reported (FAO 2010). An extensive system of protected areas was implemented in the 1960s, with protected sites now covering over 15% of the country. However, these sites were often already heavily-degraded due to logging or to provide land for agriculture (Elliott *et al.* 2003). In 1993, the Royal Forestry Department launched a project to replant 8,300 km^2 of degraded forest land nation-wide with native forest tree species, to celebrate His Majesty King Bhumibol Adulyadej's Golden Jubilee (Elliott *et al.* 2002; Elliott *et al.* 2003). Since 1994, the Forest Restoration Research Unit (FORRU) of Chiang Mai University has been working on a number of projects to restore the forests of northern Thailand. Data collected from one of these projects forms the basis of this study.

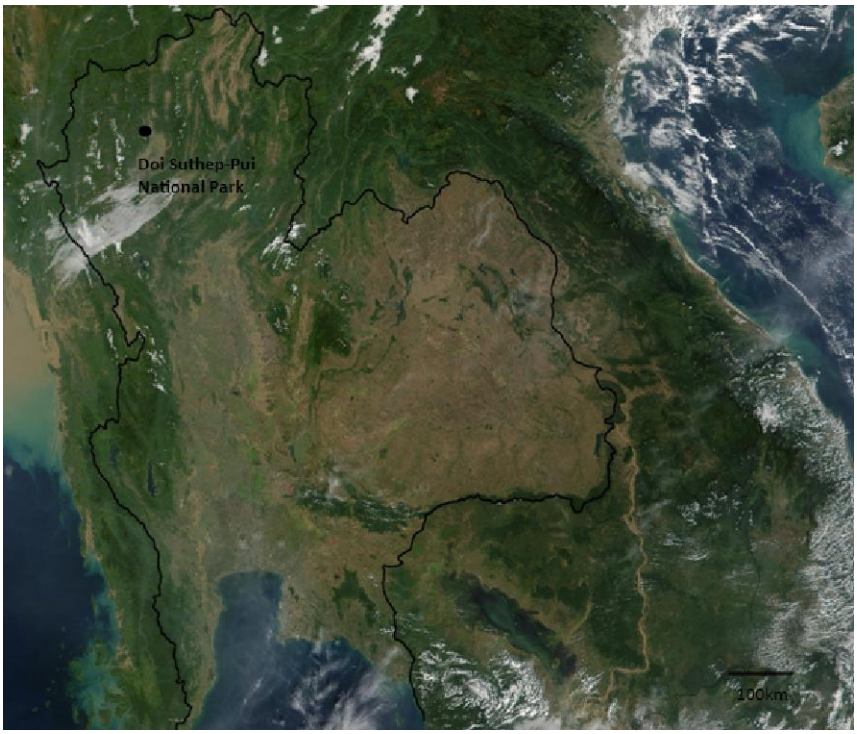


Figure 1.2: Satellite image of northern Thailand (border marked): NASA 2005. The brown area indicating deforestation clearly follows the Thai border with Cambodia to the south, Laos to the east, and to a lesser extent, Myanmar in the North West. Doi Suthep-Pui National Park is marked.

1.4. Aims and structure of this project

1.4.1. Aims

Whilst the work of FORRU has looked at the performance of individual species as framework species (Elliott *et al.* 2003), there has been little work on any characteristics that these species might share. The ultimate aim of this project is to determine whether functional trait analysis could be used to predict the results of the nursery and field trials by linking successful performance to specific species traits. If successful, this would allow pre-trial species selection and a corresponding reduction in the number of trials required. It would also provide an insight into the ecological strategies most compatible with good framework species.

This project will consider the results of restoration trials using the Framework Species Approach in northern Thailand and the functional traits of species planted in those trials to;

(a) Assess how species functional traits adhere to predictions of trade-offs and life-history strategies under a variety of ecological models and to what extent this may provide information on the limiting factors and life-history strategies exhibited by woody species in the seasonally-dry tropical forest of northern Thailand.

(b) Predict the performance of species planted as part of a restoration project in Doi Suthep-Pui National Park using known ecological models, functional traits collected in the field and environmental data such as rainfall.

(c) Assess whether consideration of functional traits and performance can provide evidence for better species selection or restoration plot management in the future

In this way, it is hoped that other projects using the same techniques may be able to reduce their dependence on costly and time consuming trials by focusing their attention on species which have been pre-identified as having “good” Framework Species traits and to tailor management regimes to improve species performance. Ultimately, the project will provide a valuable biological/ecological underpinning of a novel approach to restoration ecology. The research will advise ecological restoration of tropical forests worldwide.

1.4.2. Chapter outlines

Chapter 2: This chapter describes the field site and data sources used for this project and the processes through which these sources were collated into a single database. A link to the main database is provided.

Chapter 3 and 4: These chapters explore functional traits (Chapter 3- leaf traits and Chapter 4- wood traits) of 54 species of tree found within the Doi Suthep-Pui National Park to identify trade-offs and axes of variation between traits linked to predictions from the literature.

Chapter 5: This chapter attempts to determine whether observed relationships between growth and survival in the field for species planted from 1998 to 2001 as part of a restoration project in northern Thailand are supportive of predictions of the CSR and pioneer/climax ecological strategy models.

Chapter 6: This chapter considers seed traits in relation to each other and performance in the field and nursery in an attempt to assess the validity of predictions from the literature.

Chapter 7: This chapter uses key functional leaf and wood traits identified in Chapters 3 and 4 as the basis for modelling growth in 1998, 1999 and 2001 plots over the second season after planting.

Chapter 8: This chapter uses information derived from all chapters to look at the co-occurrence and tradeoffs between leaf, wood and seed functional traits on an entire plant basis. It uses this as the basis for describing aspects of performance in the field and nursery, especially in the 1999 and 2000 plot where performance was significantly different to in other years (as explored in Chapter 7).

Chapter 9: Concluding remarks and an assessment of potential future research.

2. Research site, data sources and database methods

2.1. Forest restoration project in Doi Suthep-Pui National Park

2.1.1. Doi Suthep-Pui National Park

The Doi Suthep-Pui National Park (created in 1981) has an area of 260 km^2 and is situated near Chiang Mai in Northern Thailand (Fig. 2.1). The park contains and is named after the two mountain peaks of Doi Suthep and Doi Pui and ranges from 340 to 1680m a.s.l. (Maxwell & Elliott 2001)

Figure 2.1: Map of Doi Suthep-Pui National Park in northern Thailand.

Whilst annual rainfall in northern Thailand is high, it is highly variable. In January and February, mean monthly rainfall can be as low as 6 mm a month, rising at the start of the monsoon in April or May to a peak of 275mm in August before dropping swiftly from October (Fig. 2.2b). The dry season is sub-divided into the cool-dry season (November–January) where maximum temperatures range from 30 ^{o}C to 32 ^{o}C and the hot-dry season (February– April), with a maximum daily temperature of between 30 ^{o}C and 39 ^{o}C, (Fig. 2.2a). April, therefore, as a time of high daily temperatures and low rainfall is a time of particular drought stress for forest species before the monsoon rains, which usually starts in May (Information Services - Thai Meteorological Office-personal communication 2013).

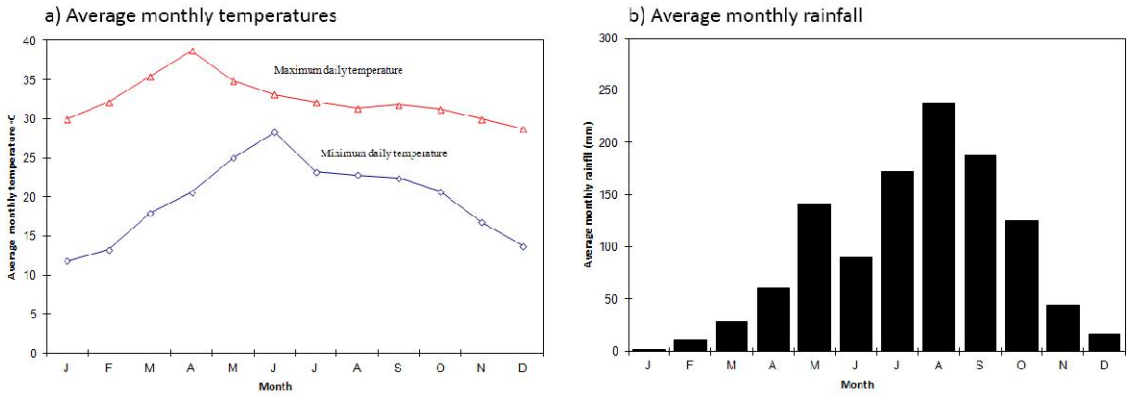


Figure 2.2: Monthly (a) maximum and minimum daily temperature and (b) rainfall in the Chiang Mai area of northern Thailand. Based on records from between 1952 and 1997– (Maxwell & Elliott 2001)

As well as strong seasonal variations, inter-annual rainfall patterns can vary significantly, both in total rainfall and rainfall patterns; in particular, the intensity, starting point and duration of the monsoon season in May, where rainfall can vary between 400mm in 2007 to 52mm in 2010 (Information Services - Thai Meteorological Office-personal communication 2013).

Below 1000 m within the park, the forest consists mainly of mixed deciduous forests and some dipterocarp forests, with some dry evergreen forests in valleys and by water sources. Above, 1000 m, Hill Evergreen forests cover most of the National Park (Maxwell & Elliott 2001). However, there are some small areas of Pine forests around Doi Pui Mountain. The area has experienced serious forest loss and degradation due to clearance for opium and rice cultivation (Maxwell & Elliott 2001).

2.1.2. Forest restoration in Doi Suthep-Pui National Park

Ban Mae Sa Mai is a Hmong village with a population of 1,700 within the boundaries of Doi Suthep-Pui National Park. As the village was settled before the park was established, the villagers of Ban Mae Sa Mai are allowed to practice agriculture within its borders. As more land was cleared for crops during the 1980s, it began to affect the water supply for the village, as well as other settlements further downstream. In addition, there was increased soil erosion and landslides as well as a loss of wildlife from the area (Elliott *et al.* 2002). As the effects of deforestation became clear in the early 1990s, the villagers of Ban Mae Sa Mai decided to address the problem.

Working with the parks authority, penalties such as fines were agreed, and enforced, for any villager discovered hunting or felling trees. The village was introduced to the Forest Restoration Research Unit (FORRU) based at Chiang Mai University. FORRU and the villagers of Ban Mae Sa Mai began to work together to preserve the remaining forest, and restore some degraded areas to functioning forest through a replanting scheme (Elliott *et al.* 2002).

FORRU first established an office and a research nursery at the National Park's former headquarters compound. Two years later, a community nursery and field plots were established at Ban Mae Sa Mai in the Ma Sa Valley in the north of the national park, which by 2003 was producing 20,000 trees a year. In 1996, FORRU began a process of screening species for use as framework species. The most promising of these were propagated for use in field trials (Blakesley *et al.* 2002) from 1997 onwards. FORRU have extended their work to other areas of Northern Thailand as well as internationally (www.FORRU.org – Accessed 2013). Whilst very successful, this process has been time consuming, with field trials being particularly labour-intensive.

2.2. Performance data derived from FORRU's research program

Species selection, morphological measurements, germination, nursery and field trials briefly described here are fully detailed in publications from the Forest Restoration Research Unit of Chiang Mai University (Pakkad *et al.* 1999; Blakesley *et al.* 2002; Elliott *et al.* 2002; Elliott *et al.* 2003).

2.2.1. Early assessment and phenology data

Previous research on forest fragments within Doi Suthep-Pui National Park provided a list of approximately 500 tree and treelet (small trees up to about 10m tall) species within the park (Maxwell & Elliott 2001) as the basis of further research. Lone trees and forest patches were observed for information on leaf, flowering and fruiting phenology, fruiting abundance and other tree characteristics not obvious from botanical texts and individual trees were identified as potential seed sources.

2.2.2. Germination trials

A number of fruit and seed measurements were made, including seed dry weight and fruit size and type. Data on the germination and early seedling characteristics of over 400 species were analysed to identify potentially successful framework species (Pakkad *et al.* 1999). Initial germination trials were performed in the nursery, with no pre-treatment of seeds to attempt to break dormancy. Seeds were planted in trays and placed in two groups; one in full shade, and one in partial shade (approximately 40%). For each species, there were three replicate batches of 24 seeds in each light condition. Seeds were observed on a daily basis and germination recorded when seedlings broke the soil surface. From these germination records, a number of key measurements were extracted, reflecting the differing germination rates, dormancy periods and synchronicity of germination of species when in full shade and semi-shade conditions.

2.2.3. Nursery performance

Selected species from germination trials were grown on in the nursery to planting-out height. Seeds were initially germinated in trays. After pricking out, and two weeks of growth under cover, seedlings were placed outside, under black shade netting (approximately 50% of full sunlight) for 3–18 months, depending on the species until reaching planting out size (50–60 cm tall). Fertiliser was applied every three months and weeds, pests and diseases controlled as required for each species. Saplings ready for planting out were hardened off in full sunlight and dispatched in June of each year. Here, growth rate in the nursery was estimated from mean length of dormancy (MLD), time in the nursery and height measured two weeks after planting in the field.

2.2.4. Field performance

Experimental plots were established by FORRU in the north of Doi Suthep-Pui National Park in 1997 (Elliott *et al.* 2002; Elliott *et al.* 2003). The experimental plots were in a degraded watershed 3-5 km above Ban Mae Sa Mai, between 1207 and 1310 metres elevation and had been cleared for agriculture 20 years previously (Elliott *et al.* 2003). Originally, the study site had been covered with evergreen hill forest. Although a few scattered trees did remain, the area was dominated by annual weeds; the nearest extensive patch of forest lying 2-3 Km away.

Tree seedlings were raised within the FORRU nursery for between one and two years and planted in mid-June each year to allow maximum time for establishment before the beginning of the dry season. Each plot consisted of three sites each. Within each plot, there were three treatment plots and one control plot. After planting, hand weeding and application of fertiliser were carried out at intervals of between 4-6 weeks throughout the wet season. Pre- and post-planting care is described fully in Elliott et al ((Elliott *et al.* 2002). Each seedling was individually tagged for later monitoring purposes.

Whilst a variety of fertilisation and weeding regimes were tested by FORRU (see section 1.1.6), only species planted in the "Framework" plots, and therefore treated with the same regimes during each year are included here to minimize extraneous effects. Framework plots were planted in June to allow maximum growth before the onset of the dry season. About three weeks before planting, the plots were sprayed with glyphosate at manufacturer recommended levels to kill weed roots and prevent immediate regrowth. Saplings were then planted randomly at a density of 3125 ha^{-1}, with 29 or 30 species planted in each plot. One hundred grams of fertiliser (NPK 15–15–15, Rabbit Brand) was added to the bottom of each planting hole immediately prior to planting. Weeding was then carried with hand tools out three times during the rainy season at 4–6 week intervals. Immediately after weeding, further 100 g doses of fertiliser were applied to each tree. For full details of method see (Elliott *et al.* 2002)

Planted trees were monitored 2 weeks after planting, at the end of the first rainy season (November 5 months after planting), and at the end of the second rainy season (November, 17 months after planting). Measurements included height (distance from ground level to the highest meristem measured by tape measure or telescopic measuring pole); root collar diameter (measured using callipers with a vernier scale); canopy width (at widest point using a tape measure). For analysis purposes, survival and growth measures over individual seasons (e.g. S23; percentage survival over the second growing season were calculated.

2.2.5. Species selection

The species analysed here were those planted in the field between 1998 and 2001. Data from these plots were chosen because this project required comparisons of a full range of successful and unsuccessful framework species. In later years, as FORRU field trials have continued and successful species have been identified, fewer "bad" framework species have been planted, making performance in later plots less useful for comparison purposes. Whilst different species were planted in each year, many species were planted in more than one year, allowing direct comparison of performance in different plots (Table 2.1)

Table 2.1: Species of seedling planted in 1998, 1999, 2000 and 2001 as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand by the Forrest restoration research unit (FORRU). Species codes used by FORRU provided in brackets.

	Planted in each year					Planted in each year			
Species	**98**	**99**	**00**	**01**	**Species**	**98**	**99**	**00**	**01**
Bischofia javanica (S004)	ü			ü	*Garcinia mckeaniana (S128)*	ü			
Melia toosendan (S005)	ü	ü		ü	*Michelia baillonii (S138)*		ü		ü
Manglietia garrettii (S007)	ü			ü	*Nyssa javanica (S146)*	ü	ü	ü	ü
Macaranga denticulata (S009)		ü	ü		*Callicarpa arborea (S156)*		ü		
Diospyros glandulosa (S012)	ü				*Heynea trijuga (S157)*	ü	ü	ü	ü
Sapindus rarak (S013)	ü	ü	ü	ü	*Machilus bombycina (S163)*		ü	ü	
Balakata baccata (S015)		ü	ü		*Glochidion kerrii (S179)*		ü		
Hovenia dulcis (S018)	ü	ü	ü	ü	*Markhamia stipulata (S204)*	ü		ü	
Rhus rhetsoides (S019)		ü	ü	ü	*Cinnamomum caudatum (S207)*		ü		ü
Ficus benjamina (S029)		ü	ü	ü	*Cinnamomum iners (S218)*	ü			
Acrocarpus fraxinifolius (S031)		ü			*Horsfieldia thorelii (S236)*	ü	ü		
Ficus subulata (S039)		ü	ü	ü	*Phoebe lanceolata (S268)*	ü			
Betula alnoides (S048)			ü	ü	*Castanopsis tribuloides (S269)*			ü	
Aphanamixis polystachya (S060)	ü				*Castanopsis acuminatissima (S270)*		ü	ü	ü
Quercus semiserrata (S062)	ü	ü	ü	ü	*Lithocarpus elegans (S280)*			ü	ü
Spondias axillaris (S066)	ü			ü	*Ficus semicordata (S315)*			ü	
Prunus cerasoides (S071)	ü	ü	ü		*Erythrina subumbrans (S317)*	ü	ü	ü	ü
Ficus altissima (S072)	ü		ü	ü	*Eugenia albiflora (S325)*	ü			ü
Gmelina arborea (S078)	ü	ü	ü		*Castanopsis calathiformis (S335)*	ü			
Morus macroura (S081)			ü		*Lithocarpus fenestratus (S337)*		ü		
Eurya acuminata (S086)	ü				*Ficus glaberrima (S361)*		ü	ü	ü
Pterocarpus macrocarpus (S092)		ü			*Ficus racemosa (S365)*		ü	ü	ü
Alseodaphne andersonii (S101)	ü				*Ficus superba (S368)*			ü	
Helicia nilagirica (S104)	ü		ü	ü	*Ficus abellii (S370)*			ü	
Sarcosperma arboreum (S105)	ü			ü	*Ficus heteropleura (S372)*		ü		
Horsfieldia amygdalina (S119)	ü	ü			*Phoebe cathia (S379)*		ü		
Aglaia lawii (S123)	ü				*Ficus hispida (S380)*		ü		

2.3. Functional Trait data

Functional trait data were both collected from the field and collated from a number of existing sources.

2.3.1. Identifying potentially useful functional traits

The attributes desirable for the Framework Species Approach were considered, and were specified as the following eight characteristics: (1) Fast germination, (2) Reliable germination, (3) High Field Survival, (4) Fast Field Growth, (5) Dense crown, (6) Early flowering/fruiting, (7) Reliable flowering/fruiting and (8) Abundant flowering/fruiting. Previous studies were also found which identified key functional traits both generally (Cornelissen *et al.* 2003) and within seasonally-dry tropical forest (Chaturvedi, Raghubanshi & Singh 2011).

As part of this process, common trade-offs between traits (Grime 1977; Swaine & Whitmore 1988; Chave *et al.* 2009) were identified as well as collections of species traits linked to particular strategies such as shade and drought tolerance and avoidance (Levitt 1972; Abrams 1994; Kitajima 1994; Bloor & Grubb 2003; Poorter *et al.* 2010; Wright *et al.* 2010). Appropriate ecological models and species strategy groups were also identified (Grime 1977; Westoby 1998).

Traits were then assessed based on their potential as good indicators, their ease and practicality of collection and their unique value. I.e. whether another, more easily collected trait may be an appropriate proxy for them. Where data required field collection, an appropriate method was identified. A literature search was carried out to identify any existing sources of trait data (Table 2.2) for the species of interest.

As part of this process, a full list of species synonyms was created and stored within the database (see database model for details) to allow the easy extraction of functional trait data from available data sources.

2.3.2. Existing data sources

A number of key data sources were identified (Table 2.2). However, these primary sources did not provide coverage of all traits and species. Where necessary, the dataset was augmented from other existing sources (such as published papers on specific species). Samples from both the CMU Herbarium and directly from the field were also used to fill gaps in the database. Certain traits, such as leaf strength, were entirely unavailable from existing sources; so necessitating both observations and collection in the field (see method sections of chapters 3, 4 and 6 for details).

Table 2.2: Existing primary data sources used as the basis of this project along with a brief description of their content and scope.

Data Source	Description of data
FORRU (FORRU,2011) and Chiang Mai University Herbarium Databases (CMU, 2011)	Contains phenological information, performance data and directly measured fruit and seed trait data. Most other trait data have been collated from existing sources and are therefore duplicates.
Royal Botanic Gardens Kew Seed Information Database (Royal Botanic Gardens Kew 2008)	Contains excellent fruit and seed functional trait data. However, limited species coverage. Valuable indication of traits by genus and family to act as confirmation
The Flora of Thailand (Flora of Thailand Editorial Board 1970+)	Only 30 of the 54 species are included within this flora
The Flora of China (Zhengyi, Raven & Deyuan 1994+)	Whilst species and trait coverage is good, some of the traits differ significantly from those recorded in the Flora of Thailand, suggesting either geographical variation or phenotypic plasticity. Is therefore appropriate mainly as a secondary source.

2.3.3. Functional trait data collation and reorganisation

Traits available, either entirely or partly, from existing sources were collated into a single MS Access database. Due to possible discrepancies between data sources, in all cases, matching records from at least two sources were required. Where only a single dataset was available, different sources were in conflict or data were not available in existing sources, data were collected from the Chiang Mai University herbarium and field observations within Doi Suthep-Pui National Park. Where field observations were made, at least five replicates were collected and compared.

Much of the information from existing data sources was highly descriptive and inappropriate for analysis. For instance, leaf trichomes are linked to drought tolerance and therefore, an important trait to consider in the analysis. However, there are many descriptive terms for the quantity, colour, shape, amount and duration of trichomes on a leaf. Using a full description of leaf hairiness resulted in as many categories as there were species in the dataset. However, identifying leaves as either “hairy” or “non-hairy” grouped clearly “very different” leaves into the same category. Quantifying data of this type was a vital stage prior to analysis. However, it was important to ensure that important information was not lost. The balance between retaining too much irrelevant data and discarding potentially important information was difficult to maintain but was assisted by extensive consideration of the role and function of specific traits when considering their categorisation.

Where possible, a trait was expressed as an objective **numerical value**, e.g. leaf shape was broadly expressed through the ratio of leaf length to leaf width. Where potential trait relationships had been identified in the literature and were appropriate, the **established grouping** used within that originating study was used. **Natural Groupings** were used to assign different species to categories. Functional categories were assigned to traits with the aim of having no more than ten categories for each trait, with no category containing fewer than two species.

Where there was no natural grouping or where it was unclear where category distinctions should fall, **multiple categorisations** of the same data may have been used. This was particularly true of data that appeared hierarchical in nature. For instance, species such as *Melia toosendem* could be described as having either compound or pinnate leaves. Both a two category system (simple and compound) and a 5 category system (Simple-unlobed, Simple-lobed, Trifoliate, pinnate, bi-pinnate) system may be appropriate. Therefore, both the detailed and grouped term were used in the analysis but care taken that these were not mistaken for independent variables.

2.3.4. The Database

The database and the functional relationships between the tables are described in Fig. 2.3. Two versions of this database are available, the first containing only collated and cleaned data (Electronic Appendix A), and the other containing raw data prior to cleaning. A general description of the database model is provided below;

The **Species table** contains the name and family of every species within the database. The primary key of this table (Species_ID) is the primary key of all data tables.

Reference tables: Reference tables provide lists of terms referenced in other tables (such as list of habitat types). In addition to the lookup tables, there are two other references tables (Data Sources and Measurements) which provide useful metadata and are not included in the referential database structure.

Species Trait Data: Data collated from a number of sources, such as flora, herbarium, field observation etc. as well as collected in the field. Includes derived fields that are either calculated from other fields (e.g. SLA is leaf area over leaf mass) or fields where there has been grouping or reallocation of traits. All tables have been summarised and contain a single row for each species with species code as a primary key. For ease of access, data have been divided into a number of tables relating to a specific part or aspect of the tree, such as seed traits; leaf traits etc.

Performance data: Data from these tables has been primarily extracted from the FORRU database (FORRU, 2011) and contains germination, nursery and field performance data.

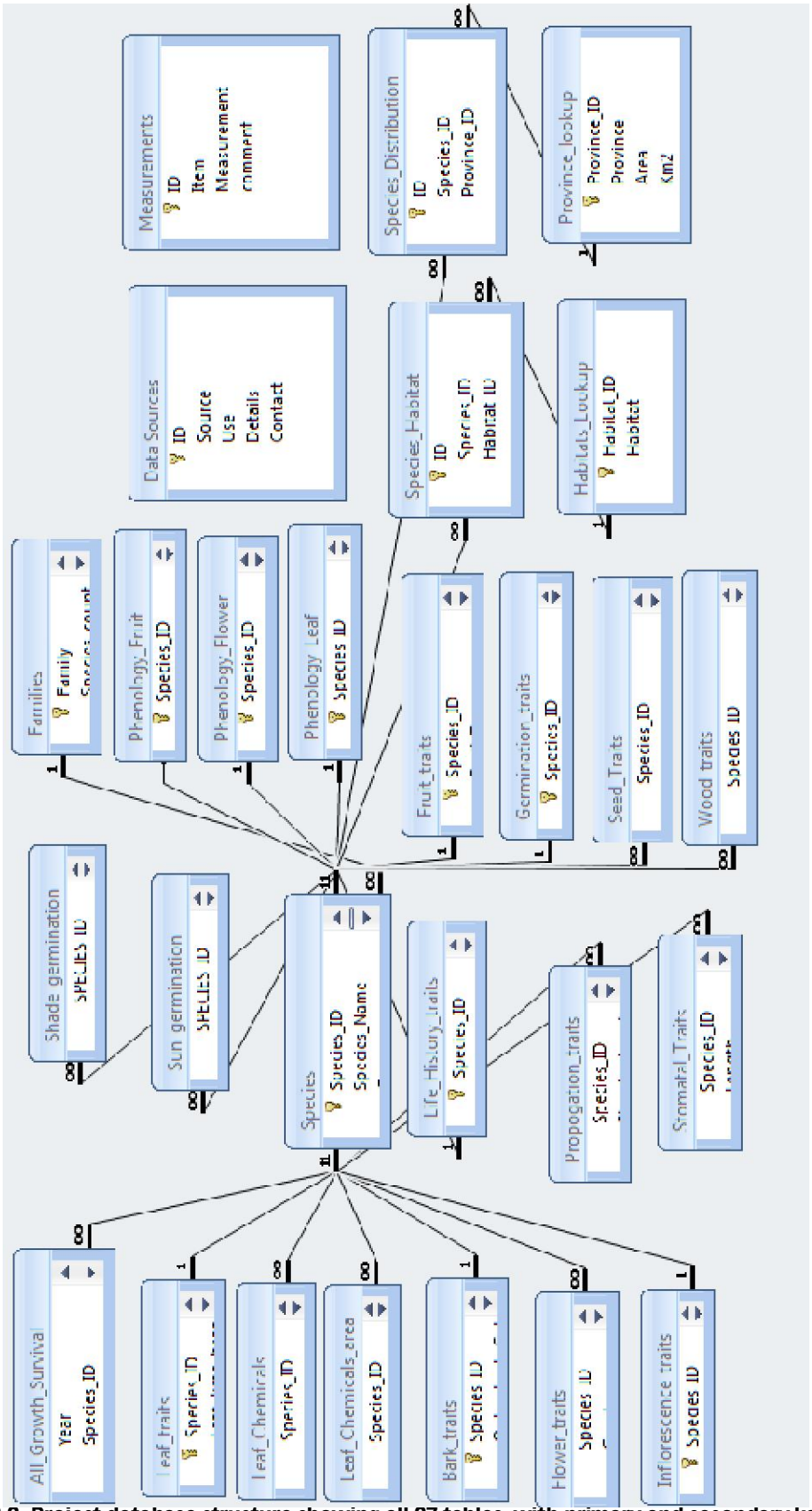


Figure 2:3: Project database structure showing all 27 tables, with primary and secondary keys. The Species_ID key , as provided in the Species table is used as a secondary key for 21 tables containing trait, phenology, distribution and performance data. Additionally, there are lookups for the habitat and distribution tables and two tables containing metadata on data sources and calculations used to derive measurements used elsewhere.

3. Co-ordination and trade-offs of leaf traits in seasonally-dry tropical forest

3.1. Introduction

3.1.1. The leaf economic spectrum

The primary function of a leaf is to sequester carbon through photosynthesis. However, leaves are vulnerable to damage through such mechanism as herbivory, mechanical damage, drought stress and heat damage. To prevent biomass loss, ie to allow a long leaf lifespan, a wide variety of protective leaf traits have evolved, but these create additional costs for the plant, per unit of photosynthesising area. A trade-off between leaf traits linked to emphasising biomass gain through the creation of maximum photosynthetic area at minimal cost of leaf mass, and those emphasising biomass retention through traits that increase leaf lifespan is theorized in the leaf economic spectrum (Wright *et al.* 2004) which proposes a variety of plant traits which vary on single axis. (Fig. 3.1).

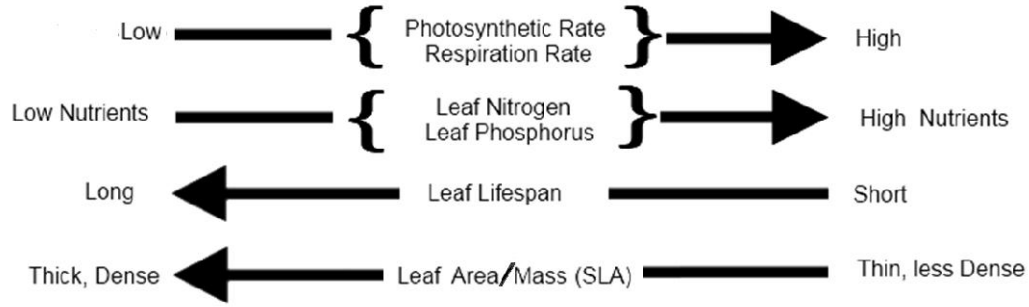


Figure 3.1: A summary of the Leaf Economic Spectrum after Wright (2004) and Shipley et al. , showing the leaf traits classically associated with the prioritising of fast biomass gain to the right and the prioritising of the retention of existing biomass on the left.

3.1.2. Maximising biomass gain

To gain biomass, leaves must absorb light energy and convert it to energy through photosynthesis. To achieve the maximum biomass gain for minimal investment of mass, the leaf will invest heavily be thin and less dense with a high SLA and minimal investment in non-metabolic features such as structural support or protection. This is reflected in high Nitrogen and Phosphorus concentrations.

3.1.3. Minimising biomass loss

Wright referred to a direct relationship between "robustness" and leaf lifespan. The term "robustness" as used here describes the investment in traits that aid the plant in retaining leaf biomass in the face of abiotic and biotic threats (Wright *et al.* 2004). Within seasonally-dry tropical forest, drought during the dry season and increasingly pathogens and herbivore damage have been recognised as such threats (Brenes-Arguedas, Coley & Kursar 2009). There are a number of different leaf characteristics that may be described as forms of robustness, some of which are outlined below;

(a) Leaf mechanical strength

Leaf mechanical strength is associated with extending leaf life-span by preventing mechanical damage and reducing herbivory (Hanley *et al.* 2007; Onoda *et al.* 2011) and is usually assessed by measuring the force to punch a hole or needle through a leaf (Matsuki & Koike 2006; Alvarez-Clare & Kitajima 2007; Kitajima & Poorter 2010). However, the importance of other types of leaf mechanical strength, such as tensile strength has not been as explored actively in relation to leaf life-span.

(b) Anti-herbivory and anti-pathogen traits

As well as mechanical strength, a number of leaf traits have been identified as anti-herbivory traits such as spines or trichomes, latex, phenols and herbivore avoidance through leaf drop (Moles *et al.* 2013). The role of calcium as an anti-fungus and anti-herbivory trait has also been described (McGuire & Kelman 1984; McGuire & Kelman 1986; Olsson 1988; Bain, Millard & Perombelon 1996; Elmer, Spiers & Wood 2007).

(c) Heat and drought tolerance traits

Sunlight interception can lead to leaf internal temperatures far greater than ambient temperatures causing a reduction in biological mechanisms and irreversible heat damage. Maintenance of leaf temperature within tolerable limits can be achieved by (a) minimising heat gain through minimising light exposure (through smaller leaves, leaf orientation or growth beneath the canopy) and (b) maximising heat loss. Heat loss through transpiration (evaporation) is a primary mechanism, especially where water is not a limiting factor. However, in times of water stress, this may be in conflict with the need to retain water. Maximising heat loss through conduction can be achieved by making leaves thinner and less dense. It has also been suggested that leaf shape can affect the efficiency of heat conductance; with smaller leaves, lobed and compound leaves, or those with a serrated or wavy leaf margins, being more efficient at losing heat (Vogel 1968; Gottschlich & Smith 1982).

In drought conditions, plants may reduce water loss (drought avoidance); tolerate low water tissue levels; (drought tolerance) or exhibit a combination of both avoidance and tolerance traits (Levitt 1972). Drought avoidance traits include seasonal leaf drop (Tyree *et al.* 1993), waxy cuticles (Levitt 1972), trichomes (Dahlin, Brick & Ogg 1992), and improved stomatal control (Kramer & Boyer 1995). Drought tolerators exhibit traits that allow them to maintain adequate cell turgor at low water levels (Munns 1988; Save *et al.* 1993). Tolerance to water stress has been attributed to osmotic adjustment and changes in cellular/tissue elasticity (Kramer & Boyer 1995; Turner 1997).

3.1.4. Shade as a limiting factor

Under the canopy, the amount of light available for photosynthesis is reduced and shade becomes a limiting factor. Some species avoid this limitation by growing only in unshaded areas and by completing their lifecycle before other species are able to shade them out. A variation on this includes early leaf flushing in deciduous forests. Shade avoidance methods include the elongation of stems and petioles and the relocation of resources to stems in order to raise leaves above the canopy (ref). Species that survive under the canopy may be referred to as shade tolerant. Two hypotheses related to shade tolerance have been proposed:

(a) the maximization of net carbon gain in low light (Givnish 1988) - where light interception is maximised through having larger, broader leaves with a high Specific Leaf Area (SLA) to provide maximum surface area for a given investment of mass. Long petioles and strong supporting structures allow the positioning of leaves to maximise light exposure (Niinemets 2004)

(b) the minimisation of biomass loss through maximising stress tolerance traits and physical robustness (Kitajima 1994).

3.1.5. Seasonally-dry tropical forests

The seasonally-dry tropical forest found in Northern Thailand, Laos and Cambodia as has a pronounced dry season between November and April. During the rest of the year, rainfall is high and drought stress unlikely to be a limiting factor. This annual drought season is an important driver of diversity, species strategy and primary productivity (Murphy & Lugo 1986). As the majority of water is lost from plants through transpiration from leaves, the influence of drought on leaf traits where the plant is under drought stress is of particular interest when considering leaf functional traits. Species within seasonally dry forest may be either deciduous or evergreen, with a deciduous leafing strategy thought to be a drought avoidance trait (Levitt 1972). Evergreen species however must have strategies to cope with drought whilst retaining their leaves during the dry season.

3.1.6. Hypotheses and aims

Here the extent to which leaf functional traits linked to fast biomass gain and biomass retention co-exist and interact within the seasonally-dry tropical forest of northern Thailand were explored within the context of the leaf economic spectrum(Wright *et al.* 2004). A number of species functional traits associated with a) the leaf economic spectrum, b) herbivore and pathogen resistance, c) drought tolerance and resistance and d) shade tolerance were collected from trees found in the seasonally-dry tropical forest of northern Thailand. It was predicted that;

- Traits associated with the leaf economic spectrum would co-vary as a single axis
- Traits associated with pathogen and herbivore resistance would co-vary with traits at the "biomass retention" end of the leaf economic spectrum.

In particular, differences between evergreen and deciduous species were investigated in the light of the importance of drought stress during the dry season in seasonally-dry tropical forests. It was predicted that;

- Traits linked to drought tolerance would occur more in evergreen than deciduous species
- Deciduous species would occur only at the "fast biomass gain" end of the leaf economic spectrum as they have a leaf lifespan of less than one year.
- Within evergreen species only, traits linked to drought tolerance and avoidance would co-vary with traits at the "biomass retention" end of the leaf economic spectrum.

3.2. Methods

3.2.1. Doi Suthep-Pui National Park

The Doi Suthep-Pui National Park (created in 1981) consists of 260 km^2 near Chiang Mai in Northern Thailand (18.83203°N / 98.88805°E) and ranges from 340 to 1680m a.s.l (Maxwell & Elliott 2001). The park is within the monsoonal belt and has a pronounced dry season (Fig. 3.1), Whilst annual rainfall is high, rainfall in January and February can be as low as 6 mm a month, rising after the start of the monsoon in April or May to a peak of 275mm in August before dropping swiftly from October. The dry season is subdivided into the cool-dry season (November–January) where maximum temperatures range from 30 ^{o}C to 32 ^{o}C and the hot-dry season (February– April), with a maximum temperature daily temperature of between 30 ^{o}C and 39 ^{o}C (Information Services - Thai Meteorological Office-personal communication 2013).

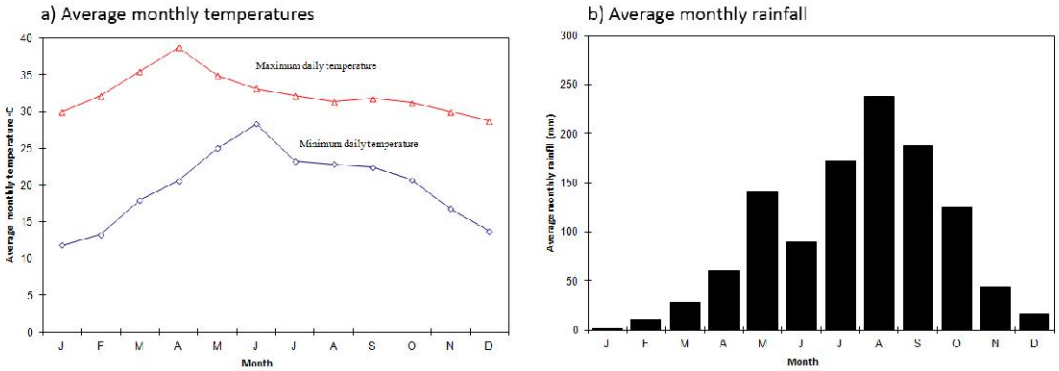


Figure 3.2: Monthly (a) maximum and minimum daily temperature and (b) rainfall in the Chiang Mai area of northern Thailand. Based on records from between 1952 and 1997– (Maxwell & Elliott 2001)

The forests of Doi Suthep-Pui National Park can be described as seasonally-dry tropical forest. Below 1000 m within the park, the forest consists mainly of mixed deciduous forests and some dipterocarp forests, with some dry evergreen forests in valleys and by water sources where water supply is more available. Above 1000 m, Hill Evergreen forests cover most of the National Park (Maxwell & Elliott 2001). Whilst the forests themselves are evergreen, species may either be evergreen or deciduous, with deciduous species losing their leaves during the annual drought.

3.2.2. Species selected

Species used here consisted of 54 species planted as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand between 1998 and 2001 (Table 3.1). The species for which data have been collected covered 23 families, with many families containing only a single representative. Species were placed in four broader groups (clades). i.e.(Rosids, 35 species; Asterids, 7 species; Eudicots, 1 species and Magnoliids, 10 species using the Angiosperm phylogeny Group System 111 (Bremer *et al.* 2009).

Table 3.1: The 54 species of tree (with corresponding species code and clade) found in Doi Suthep-Pui National Park from which leaf trait data has been collected for this project.

Species_Name	Code	Clade	Species_Name	Code	Clade
Acrocarpus fraxinifolius	S031	Rosids	Garcinia mckeaniana	S128	Rosids
Aglaia lawii	S123	Rosids	Glochidion kerrii	S179	Rosids
Alseodaphne andersonii	S101	Magnoliids	Gmelina arborea	S078	Asterids
Aphanamixis polystachya	S060	Rosids	Helicia nilagirica	S104	Eudicots
Balakata baccata	S015	Rosids	Heynea trijuga	S157	Rosids
Betula alnoides	S048	Rosids	Horsfieldia amygdalina	S119	Magnoliids
Bischofia javanica	S004	Rosids	Horsfieldia thorelii	S236	Magnoliids
Callicarpa arborea	S156	Asterids	Hovenia dulcis	S018	Rosids
Castanopsis acuminatissima	S270	Rosids	Lithocarpus elegans	S280	Rosids
Castanopsis calathiformis	S335	Rosids	Lithocarpus fenestratus	S337	Rosids
Castanopsis tribuloides	S269	Rosids	Macaranga denticulata	S009	Rosids
Cinnamomum caudatum	S207	Magnoliids	Machilus bombycina	S163	Magnoliids
Cinnamomum iners	S218	Magnoliids	Manglietia garrettii	S007	Magnoliids
Diospyros glandulosa	S012	Asterids	Markhamia stipulata	S204	Asterids
Erythrina subumbrans	S317	Rosids	Melia toosendan	S005	Rosids
Eugenia albiflora	S325	Rosids	Michelia baillonii	S138	Magnoliids
Eurya acuminata	S086	Asterids	Morus macroura	S081	Rosids
Ficus abelli	S370	Rosids	Nyssa javanica	S146	Asterids
Ficus altissima	S072	Rosids	Phoebe cathia	S379	Magnoliids
Ficus benjamina	S029	Rosids	Phoebe lanceolata	S268	Magnoliids
Ficus glaberrima	S361	Rosids	Prunus cerasoides	S071	Rosids
Ficus heteropleura	S372	Rosids	Pterocarpus macrocarpus	S092	Rosids
Ficus hispida	S380	Rosids	Quercus semiserrata	S062	Rosids
Ficus racemosa	S365	Rosids	Rhus rhetsoides	S019	Rosids
Ficus semicordata	S315	Rosids	Sapindus rarak	S013	Rosids
Ficus subulata	S039	Rosids	Sarcosperma arboreum	S105	Asterids
Ficus superba	S368	Rosids	Spondias axillaris	S066	Rosids

3.2.3. Leaf trait data collection

Both deciduous and evergreen species can be found within the Doi Suthep-Pui National Park, with deciduous species losing their leaves during the annual drought. There are in addition some species which display "Intermediate" behaviour such as facultative leaf loss only during extreme drought, annual leaf exchange or a very brief deciduous period.

Phenological leafing strategy data (deciduous, evergreen or intermediate) were collated from the Chiang Mai University Herbarium Database (CMU, 2011) and refers to leafing patterns within the Doi Suthep-Pui National Park itself. Other sources such as the Flora of China (Zhengyi, Raven & Deyuan 1994+) and the Flora of Thailand (Flora of Thailand Editorial Board 1970+) often stated different strategies to those displayed within Doi Suthep-Pui National Park, suggesting that a number of species identified as either evergreen or deciduous may actually be facultative deciduous species.

Leaf trait and related data (Table 3.2) were collected during 2011 from 54 species of tree within Doi Suthep-Pui National Park. Samples were collected during the wet season and consisted of shade leaves from at least 4 different trees per species. Leaves were placed in plastic bags containing damp tissue paper immediately on collection and processed within 24 hours.

Immediately after a leaf was picked, a note was made of latex content, margin and leaf type. Leaves were then examined using a hand lens for the presence of trichomes.

Leaves were flattened under glass and photographed against a white background with an appropriate scale. They were then weighed, before being dried at 70°C for 72 hours and then weighed again to obtain wet weight, dry weight and water content data. Leaf images were analysed using ImageJ software and length from base to tip, width at the widest part of the leaf, leaf area and petiole length measurements taken.

Hand-cut sections from fresh leaves were stained with Sudan IV solution and mounted in glycerol. Leaf thickness and leaf cuticle thickness measurements were made using a microscope at a variety of appropriate magnifications.

For chemical analysis, fresh entire leaves, including the petiole, were dried at 85 ^{o}C to 90^{o}C for 24 hours, ground to pass though a 1 mm sieve and re-dried immediately before weighing. Leaf content of P, K, Ca, Mg, Na, Fe, Zn, Cu and Mn were analysed using the dry ashing method. P was analysed using an autoanalyser, K and Na using a Flame Photometer and Ca, Mg, Zn, Cu, Fe and Mn by Atomic Absorption Spectroscopy. C and N were analysed using a Carlo Erba - NC2500 elemental analyser, which uses the flash combustion method. Measurements, key ratios and derived fields identified by literature search were calculated and included in the analysis.

Table 3.2: Leaf-trait Measurements collected from 54 species of trees within the Doi Suthep-Pui National Park in Northern Thailand.

Descriptive variables (values)	Continuous variables (units)	Derived continuous variables (Calculation;Units)
Phenological leafing strategy (Evergreen, Intermediate, Deciduous)	Area (mm^2)	Specific Leaf Area (SLA) (Leaf Area/Leaf Dry Mass; $mm^2\ g^{-1}$)
	Wet Mass (g)	
	Dry Mass (g)	Leaf Density (Dry Mass/area*thickness; $g\ mm^3$)
	Blade Length (mm)	
	Blade Width (mm)	
	Petiole length (mm)	Petiole_Ratio (Petiole length/Blade length; ratio)
Glabrescence (Glabrous, Glabrescent, Hairy)	Leaf Thickness (µm)	
	Cuticle thickness (µm)	Blade_Ratio (Blade width/Blade length; ratio)
	N_{mass} ($mg\ g^{-1}$); N_{area} ($mg\ mm^{-2}$)	
	C_{mass} ($mg\ g^{-1}$); C_{area} ($mg\ mm^{-2}$)	DryWetRatio (Dry weight/Wet weight; ratio)
	P_{mass} ($mg\ g^{-1}$); P_{area} ($mg\ mm^{-2}$)	
Leaf Type (Simple, Compound)	K_{mass} ($mg\ g^{-1}$); K_{area} ($mg\ mm^{-2}$)	Nitrogen to carbon ratio (N:C Ratio) ($N_{mass}/C_{mass;}$ ratio)
	Na_{mass} ($mg\ g^{-1}$); Na_{area} ($mg\ mm^{-2}$)	
	Ca_{mass} ($mg\ g^{-1}$); Ca_{area} ($mg\ mm^{-2}$)	P:N Ratio (P_{mass}/N_{mass}; ratio)
	Mg_{mass} ($mg\ g^{-1}$); Mg_{area} ($mg\ mm^{-2}$)	
Leaf Margin (Entire, Partially-Toothed, Full Toothed)	Fe_{mass} ($mg\ g^{-1}$); Fe_{area} ($mg\ mm^{-2}$)	Stomatal cross-sectional area ((Stomatal Diameter/2)^2*pi; mm^2)
	Mn_{mass} ($mg\ g^{-1}$);Mn_{area} ($mg\ mm^{-2}$)	
	Zn_{mass} ($mg\ g^{-1}$); Zn_{area} ($mg\ mm^{-2}$)	Stomatal Proportion (Stomatal Count*Stomatal cross-sectional area; proportion)
	Stomatal Diameter (µm)	
	Stomatal Count (mm^{-2})	
	Leaf breaking point (LBP) (g)	Leaf Tensile strength (LTS) (LBP /leaf thickness;g mm-1
		Leaf Strength per Unit Mass (SPUM) (LBP*SLA; $g\ g^{-1}$)

3.2.4. Measurement of stomatal size and number

Clear nail varnish was painted thickly onto adaxial and abaxial surfaces of each leaf. When dry, a piece of clear tape was applied to the nail varnish and used to pull the nail varnish off the leaf. The resulting print was then attached to microscopic slides. Photographs of these prints were taken under X10 magnification (Fig. 3.3) and counts of stomata were made using ImageJ imaging software. Measurements of stomata were made under X50 magnification. At least five shade leaves, from five different trees were examined for each species. Stomatal cross-sectional area was calculated from stomatal length assuming stomata were round when open and stomatal proportion calculated from stomatal cross-sectional area and stomatal count (Table 3.2).

a) At X10 magnification **b) at X50 magnification**

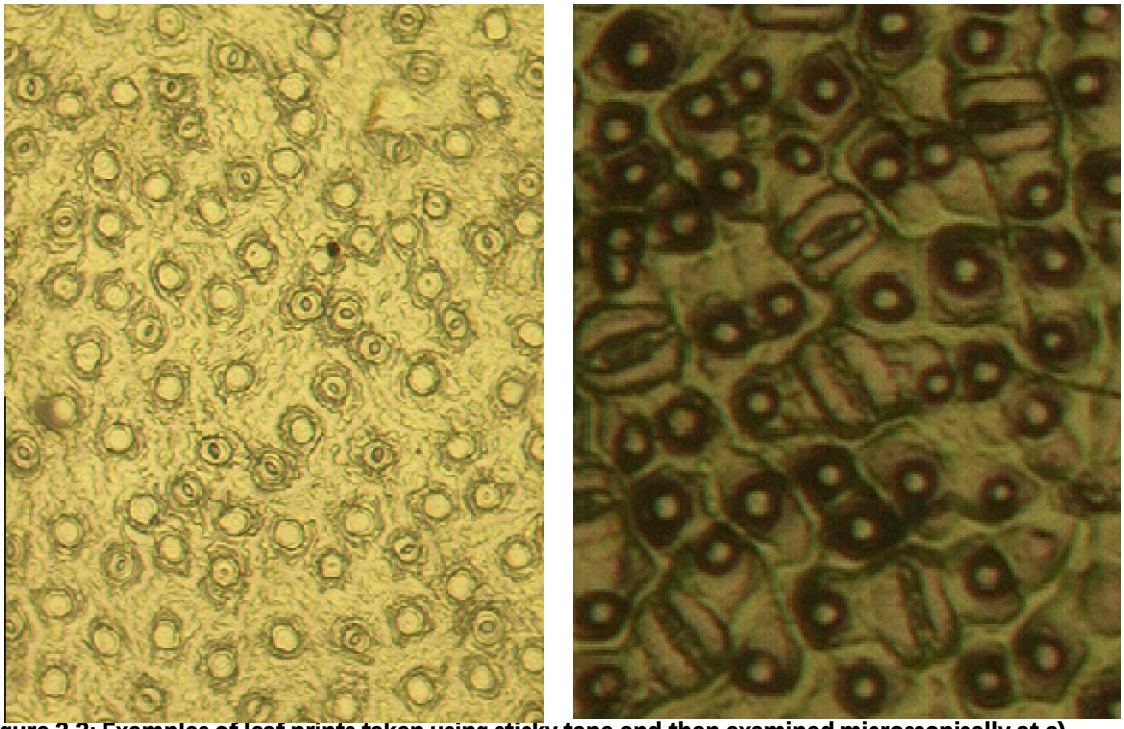


Figure 3.3: Examples of leaf prints taken using sticky tape and then examined microscopically at a) X10 magnification and b) X50 magnification used for measurement and counts of leaf stomata from 54 species of trees within the Doi Suthep-Pui National Park in Northern Thailand.

3.2.5. Measurement of leaf breaking point

Leaf breaking point was measured using an adapted version of a method detailed in Balsamo *et al*. (Balsamo *et al.* 2004) which allows accurate measurement without expensive and non-portable equipment.

A small container (made from a plastic water bottle) was suspended on string from a bulldog clip. A second bulldog clip was suspended from a hook. A piece of lamina (without central vein, 5mm wide and 20mm long) was cut longitudinally from the leaf using a scalpel, avoiding the central vein.

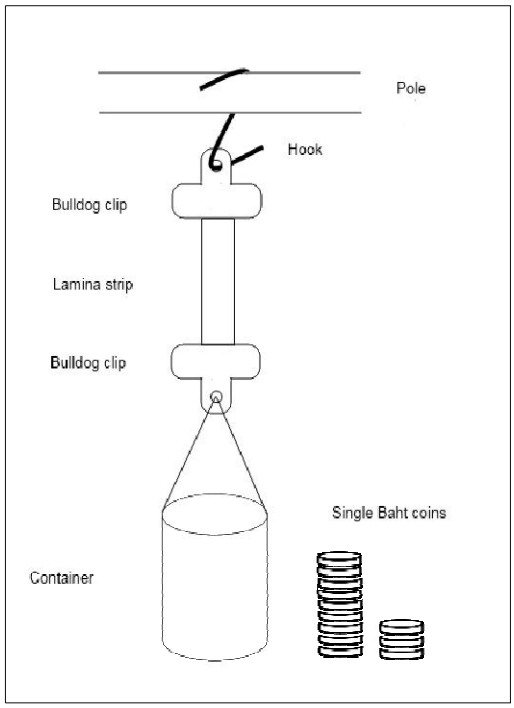


Figure 3.4: Simple apparatus used to measure the tensile strength of a piece of leaf lamina as described in Balsamo et al (2004).

The thickness of each leaf section was measured using electronic callipers. This section of leaf was held between the two bulldog clips (Fig. 3.4.). Small coins (in this case single Baht pieces) were added to the container until the lamina piece tore and the weight that can be supported by the leaf strip was recorded. This process was repeated ten times for each species; two leaves for each of 5 replicate trees, a mean taken and recorded as leaf breaking point (LBP).

As well as leaf breaking point, two derived measures were calculated:

(1) Leaf Tensile strength (LTS) = (weight supported per unit leaf thickness, g mm^{-1}) (LBP/leaf thickness)

(2) Strength per Unit Mass (SPUM) = (weight supported per unit mass, g g^{-1}) = Leaf breaking point (LBP)*Specific leaf area (SLA)

3.2.6. Statistical analyses

Correlations between continuous traits were performed using a Spearman rank correlation coefficient because the data were not normally distributed (highly skewed and presence of some outliers for most traits).

Where assessments were made of whether three or more samples differed significantly, the non-parametric method (Kruskal-Wallis one-way analysis method) was used, because of the highly-skewed nature of most of the continuous trait data used. Where two samples were compared, the Mann-Whitney U-test was used.

Generalized Linear Modeling (GLM, function 'glm') within the R statistical environment (R Development Core Team, 2012) was used to derive relationships between traits and measures of growth. All traits were normalized to a scale of 0.1 to 1.1 before analysis to account for the very large scale differences.

The parsimony protocol outlined by Crawley (2007) was used to simplify the model, i.e. by removing any redundant variables and producing the Minimum Adequate Model (MAM). Here a Gaussian error structure and a log-link function was used. This process started through fitting the maximal model which a selected subset of variables and their interactions. The sub-set selected for inclusion in any given analysis was based on (1) literature information, (2) an assessment of correlations between the dependent and all possible independent variables, and (3) an exploratory factor analysis. Thereafter, non-significant values and interaction terms were removed sequentially from the highest order interactions downwards. At each step the significance of deleted items was assessed using analysis of variance using the χ^2 statistic (Crawley 2007).

Principal component analysis (function "prcomp") was used within the R statistical environment (R Development Core Team, 2012) to derive a small number of principal components from large multi-trait datasets.

3.3. Results

3.3.1. Differences between evergreen and deciduous species

Of the 54 species considered, 16 were deciduous, 29 were evergreen and 9 had an intermediate phenological leafing strategy. Half of the deciduous trees, but only 3 (10%) of the evergreen trees had compound leaves. There were 5 deciduous species (31%) with fully-toothed margins, whereas evergreen species had mostly entire margins, with only one (3%), (*Eurya acuminata* -S086) having a fully serrated margin. In total, 4 of the 16 deciduous species had simple leaves with an entire or slightly toothed margin, whereas 25 of the 29 evergreen species had simple leaves with an entire or partly toothed margin. Of the 9 Intermediate species, 4 had simple leaves with entire margins.

No statistically-significant difference was found in cuticle thickness between evergreen and deciduous species. No significant link was found between trichomes and leaf phenological leafing strategy.

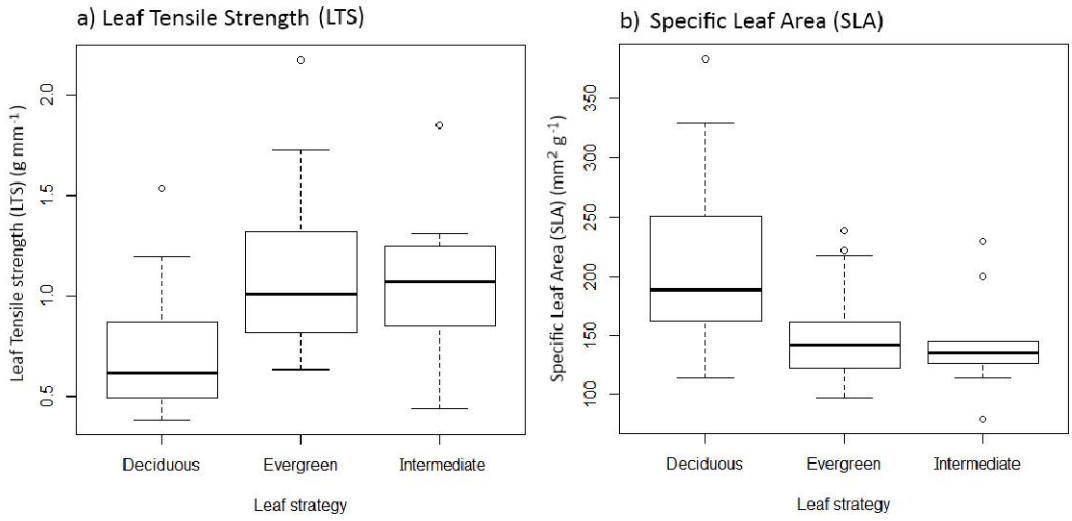


Figure 3.4: Differences in leaf tensile strength (LTS) and specific leaf area (SLA) between evergreen, deciduous and intermediate species for 54 species of tree found in Doi Suthep-Pui National Park, northern Thailand.

Deciduous species had on average higher SLA (p=0.005), higher N_{mass} (p=0.007), P_{mass} (p=0.023), K_{mass} (p=0.049), N:C Ratio (p=0.003) and water content (p=0.019) than evergreen species. They also had wider blades (p=0.009) and mechanically weaker leaves (LBP p=0.003, LTS p=0.003, SPUM p = 0.011) than evergreen species (Fig. 3.4). No difference in Ca_{mass} or Latex content was found between groups.

Many of the traits that differed between evergreen and deciduous species were correlated with SLA, and as SLA differed between evergreen and deciduous species, may have represented autocorrelations. As there was some overlap in SLA between the two groups, it was possible to create general linear models for each trait that combined both SLA and phenological leafing strategy. It was found that predictions of P_{mass}, N_{mass}, K_{mass}, N:C Ratio, blade ratio, water content and LBP were not aided by the addition of phenological leafing strategy to the models and therefore differences were due purely to SLA. However, the MAM for LTS (Table 3.3) consisted only of phenological leafing strategy, suggesting that the correlation between LTS and SLA was due only to the differing SLAs between evergreen and deciduous species.

Table 3.3: Minimum adequate general linear model predicting leaf tensile strength (LTS) from phenological leafing strategy (evergreen, deciduous and intermediate) for 54 species of tree found in Doi Suthep-Pui National Park in northern Thailand

	Estimate	St. Error	t	value	Pr(>|t|)
(Intercept)	0.25925	0.05228	4.959	9.27E-06	***
Leaf strategy - Evergreen	0.259	0.06366	4.069	0.000175	***
Leaf strategy - Intermediate	0.22836	0.08669	2.634	0.011319	*

3.3.2. Nitrogen, Phosphorus and SLA

Nitrogen concentration, phosphorus concentration and SLA were strongly correlated in both evergreen and deciduous species (Table 3.4a, Fig. 3.5). A principal components analysis of these traits created a single component that explained 75% of variation in these traits. The second principal component (13% of variation), primarily described the ratio of nitrogen to phosphorus concentration.

Table 3.4: a) Spearman correlations between nitrogen concentration, phosphorous concentration and specific leaf area (SLA) for 54 species of both deciduous and evergreen tree found in Doi Suthep-Pui National Park in northern Thailand with significnance given in brackets. b) principal components derived for the same species and traits, with contributions from each variable provided and the percentage of total variance described indicated in brackets.

a) Spearman Correlations (significance in brackets)

		Evergreen	
Deciduous	N_{mass}	0.603***(<0.001)	0.592***(<0.001)
	0.582* (0.011)	P_{mass}	0.337* (0.037)
	0.521* (0.023)	0.657* (0.004)	SLA

b) Principal components

	PC1 (75%)	PC2 (13%)	PC3 (12%)
Pmass	0.69	-0.05	-0.72
Nmass	0.5	-0.69	0.53
SLA	0.52	0.72	0.45

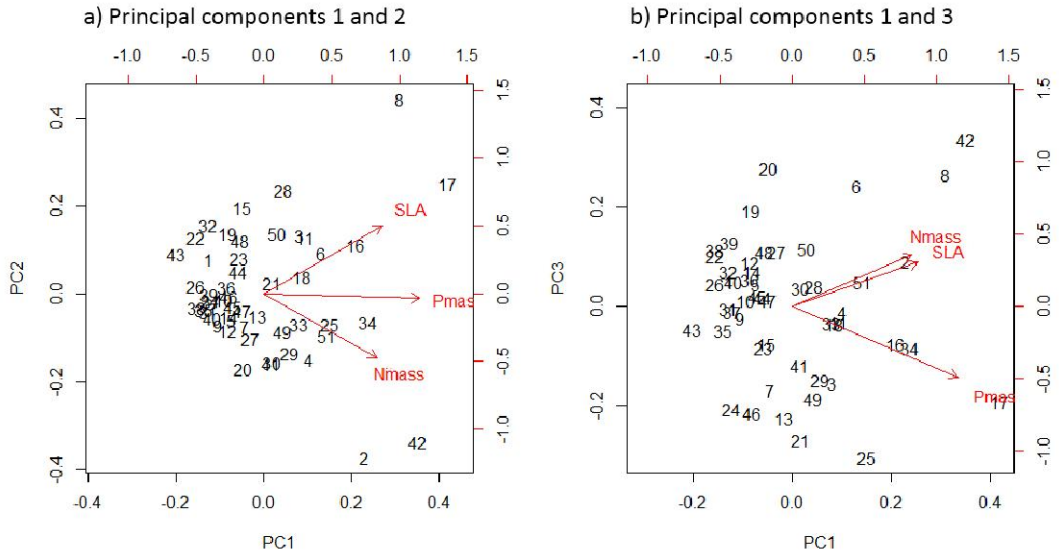


Figure 3.5: Biplots relating principal components derived from leaf nitrogen concentration, leaf phosphorous concentration and specific leaf area (SLA) for 54 species of both deciduous and evergreen tree found in Doi Suthep-Pui National Park in northern Thailand

3.3.3. Leaf Thickness and Density

In deciduous species, leaf density was correlated negatively with K_{mass} (p=0.008) and SLA (p=0.004). In evergreens, leaf density was positively correlated with Drywetratio (p<0.001) and LTS (p=0.004) but negatively with SLA, (p=0.004). There was also a negative correlation between leaf density and thickness (p<0.001) that was not found in deciduous species. However, by considering leaf thickness, it can be seen that in deciduous species, the relationship between density and thickness changes from a positive (p=0.09) to a negative (p=0.007) correlation when leaves reach approximately 160µm thickness; in thicker leaves of both evergreen and deciduous species, density and thickness were negatively correlated (Fig. 3.6).

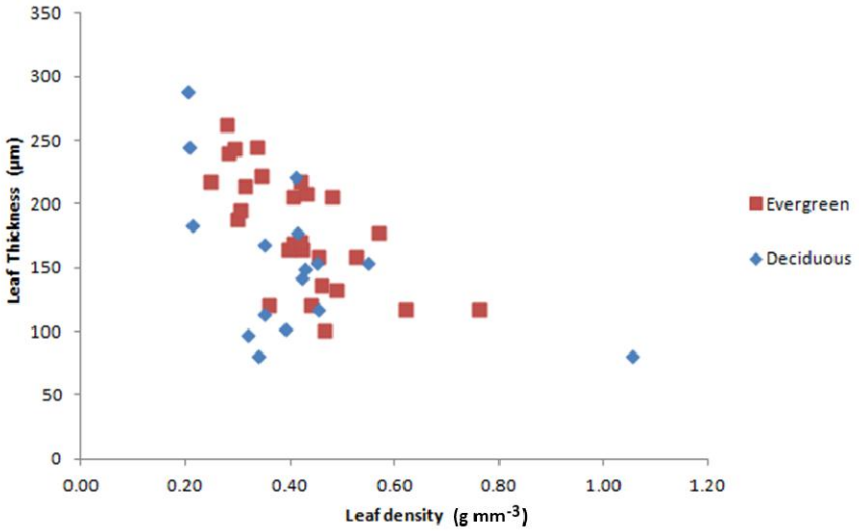


Figure 3.6: Leaf thickness and leaf density for 54 species of tree found in Doi Suthep-Pui National Park, northern Thailand, separated by phenological leafing strategy (evergreen and deciduous).

Separation of deciduous species into those with leaves thicker than 160µm and thinner than 160 µm produced only six and nine species respectively. Even with such small numbers, distinct differences in relationships were found. In thicker deciduous leaves, leaf density was negatively correlated with K_{mass} (p=0.009) and K_{area} (=0.002); relationships not found in evergreen species of a similar thickness. No correlation with Drywetratio or LTS was found, despite such relationships in evergreen species. In fact, leaf density was correlated negatively with SPUM (p=0.021). In thinner deciduous leaves, density was correlated negatively with N_{mass} (p=0.001) and N:C Ratio (p=0.004).

3.3.4. Leaf Toughness

Leaf breaking point varied considerably, with the strongest leaves supporting over ten times the weight of the weakest leaves. Leaf breaking point was greater in evergreen than deciduous species. In evergreen species, LBP was positively correlated with Mg_{area} ($p=0.007$) and in deciduous species, with Mn_{area} ($p=0.001$).

It is intuitive to suppose that Leaf breaking point would decrease as SLA decreases and a correlation was observed ($p<0.001$). However, SLA only explains 16% of the variation in LBP in both evergreen and deciduous species (Table 3.5). Thickness alone is a better predictor in deciduous species ($r^2=0.502$), and combining both leaf thickness and leaf density in a better predictor in evergreen species ($r^2=0.44$). Over 64% of variation in LBP for deciduous species was explained by differences in SPUM or LTS. It would, therefore, appear that it is differences in the physical strength properties of the leaf rather than the amount of leaf tissue that affect leaf breaking point. In evergreen species, LTS was less valuable but SPUM was still an excellent predictor (Table 3.5).

Table 3.5: Exploratory general linear models for the prediction leaf breaking point in evergreen and deciduous species using leaf traits for 54 species of tree found in Doi Suthep-Pui National Park in northern Thailand.

Phenological leafing strategy	Variables in model	Adjusted r^2 Value
Deciduous	SLA	0.161
	Thickness	0.502
	Density	No relationship
	Thickness*Density	No different to only Thickness
	SPUM	0.679
	LTS	0.645
Evergreen	SLA	0.156
	Thickness	0.249
	Density	0.030
	Thickness:Density +Density	0.446
	SPUM	0.550
	LTS	0..325

SPUM in evergreen species was correlated with positively with thickness ($p=0.023$). SPUM in deciduous species was correlated positively with Fe_{area}, ($p=0.004$) and negatively with density ($p=0.013$).

3.3.5. Length of the in-leaf period

Deciduous species had higher SLA (p=0.005), N:C Ratio and P_{mass} and lower LBP than evergreen species (Fig. 3.7).

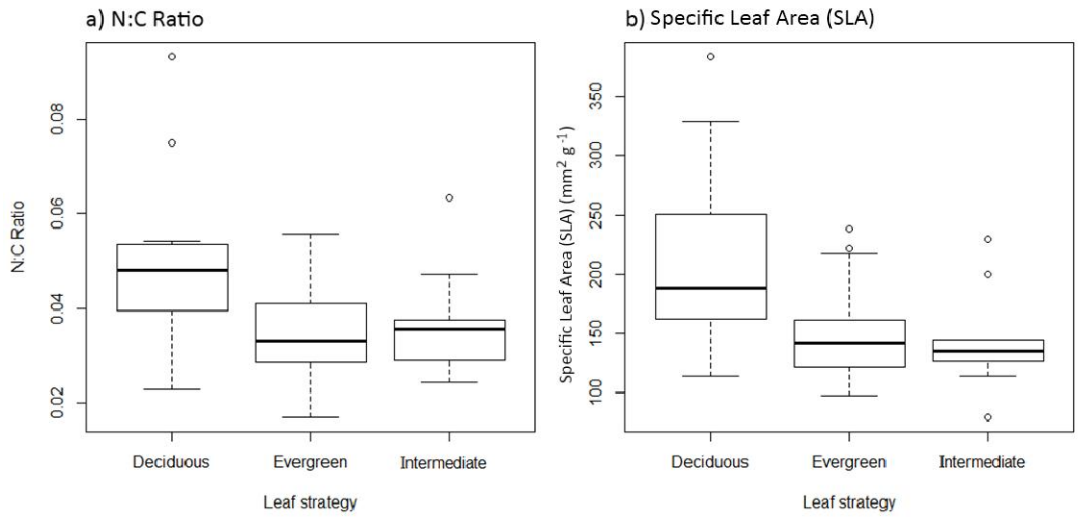


Figure 3.7: a) Nitrogen to carbon ratio (N:C Ratio) and b) Specific leaf area (SLA) for 54 species of tree found in Doi Suthep-Pui National Park, northern Thailand, separated by leafing strategy (evergreen, deciduous and intermediate).

For deciduous species, the number of months in leaf was positively correlated with leaf thickness (p<0.001), LBP (p=0.012) N_{area} (p=0.006) and negatively correlated with SLA (p=0.035). The most significantly correlated trait (leaf thickness) suggested that a leaf thickness of less than 160 µm indicated an in-leaf period of ten months or less (Fig. 3.8). In-leaf period was not correlated with N_{mass}, P_{mass} or NC Ratio. In thin leaves, leaf thickness was positively correlated with Fe_{mass} (p<0.001), in thicker leaves, leaf thickness was negatively correlated with K_{mass} (p=0.007).

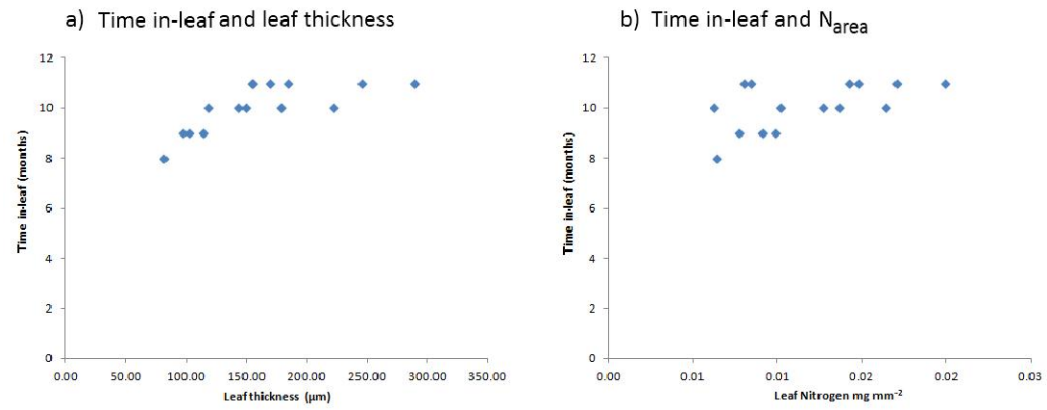


Figure 3.8: a) Leaf thickness and b) Nitrogen content by unit area (N_{area}) related to number of months in-leaf for fourteen species of deciduous tree found in the Doi Suthep-Pui National Park in northern Thailand.

3.3.6. Anti-herbivory traits

Here, species with very high Ca_{mass} also contained latex and species with very low levels of calcium did not (Fig. 3.9). However, between these two extremes, the presence of latex was more mixed. No links were found between compound leaves and latex, mechanical strength or Ca_{mass}.

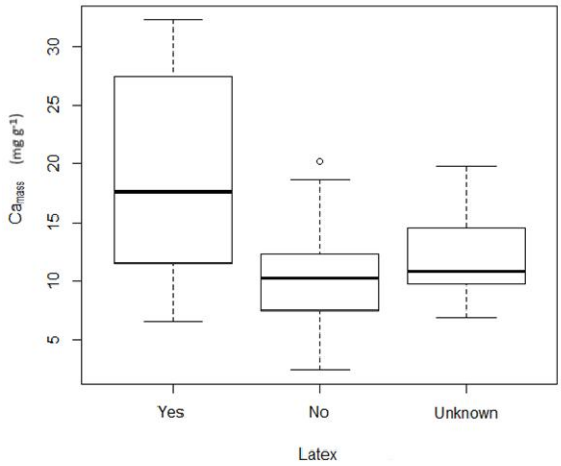


Figure 3.9: Leaf calcium content (Ca_{mass}) for 54 species of deciduous tree found in the Doi Suthep-Pui National Park in northern Thailand comparing species with leaf latex, without leaf latex and species where leaf latex content is unknown.

Trichomes, Ca_{mass}, cuticle thickness and mechanical strength (LBP, LTS or SPUM) were unrelated to each other in either evergreen or deciduous species. Ca_{mass} was correlated positively with Mg_{mass} ($p<0.001$), but only in evergreen species (Fig3.10a). In deciduous species only, Ca_{mass} was correlated positively with petiole ratio ($p = 0.016$), (Fig3.10b). In evergreen species only, cuticle thickness was negatively correlated blade length ($p=0.009$), and positively with Na_{area} ($p=0.007$),

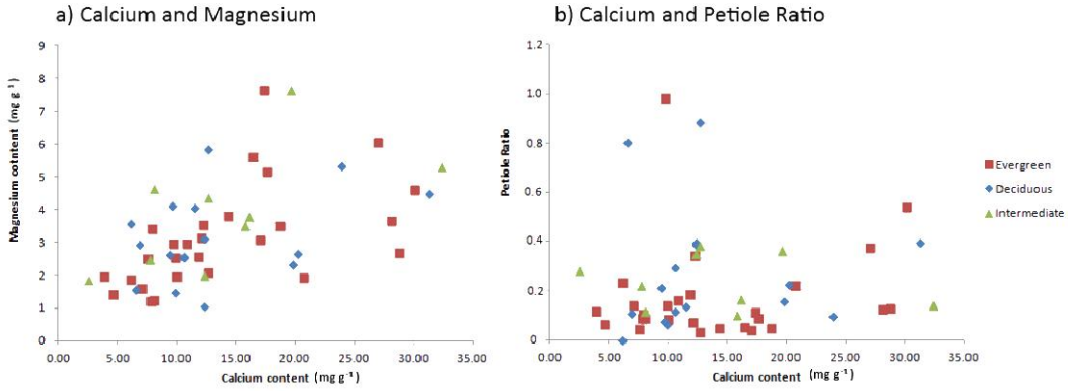


Figure 3.10: Leaf calcium content (Ca_{mass}) related to a) leaf magnesium content and b) petiole length to leaf length ratio (petiole ratio) for 54 species of deciduous, evergreen and intermediate tree found in the Doi Suthep-Pui National Park in northern Thailand.

3.3.7. Leaf thickness, margins and trichomes

Here, thinner deciduous leaves tended to have toothed margins. The same was not found in evergreen species, possibly due to the very small number of evergreen species with both very thin leaves and serrated margins (Fig. 3.11). In both evergreen and deciduous species, glabrous leaves tended to be thicker than those with trichomes. Whilst in deciduous species, this translated to a correlation with SLA, in evergreen species it did not. Glabrescent leaves were similar in thickness to leaves with trichomes on mature leaves (Fig. 3.12).

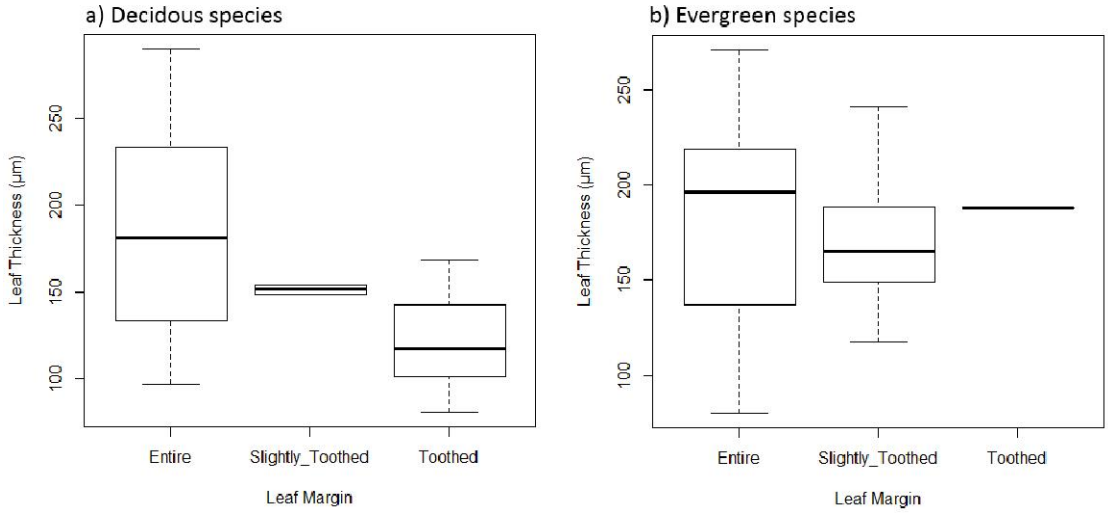


Figure 3.11: Comparison of leaf thickness in species with differing leaf margins (entire, toothed and slightly-toothed) in a) Deciduous species and b) Evergreen species for 54 species of tree fond in the Doi Suthep-Pui National Park in northern Thailand.

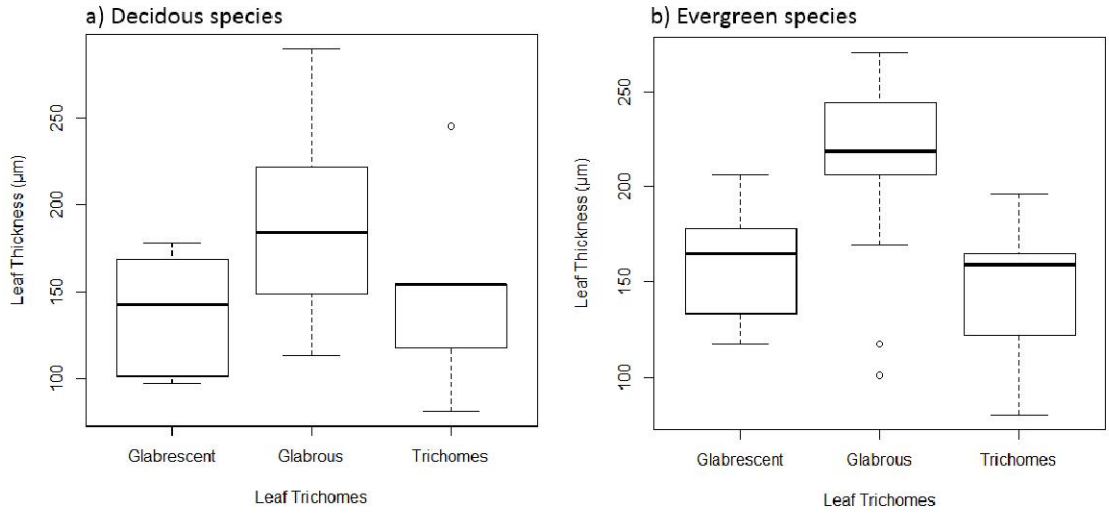


Figure 3.12: Comparison of leaf thickness in species with differing amounts of leaf trichomes (glabrous, glabrescent and with trichomes in all ages of leaf) in a) Deciduous species and b) Evergreen species for 54 species of tree found in the Doi Suthep-Pui National Park in northern Thailand.

3.3.8. Stomata

No differences in stomatal count, length or proportion were found between evergreen and deciduous species. Stomatal size and number were negatively correlated with each other but only in evergreen species (p=0.004). However, this may simply be due to the number of species for which data are available; (n=12 for deciduous species and n=18 for evergreen species as the pattern observed appears similar (Fig. 3.13a). In evergreen species only stomatal length was correlated negatively with Fe_{mass} (p=0.007) and Fe_{area} (p=0.002, Fig. 3.13b). Stomatal count was not strongly correlated with any chemical components.

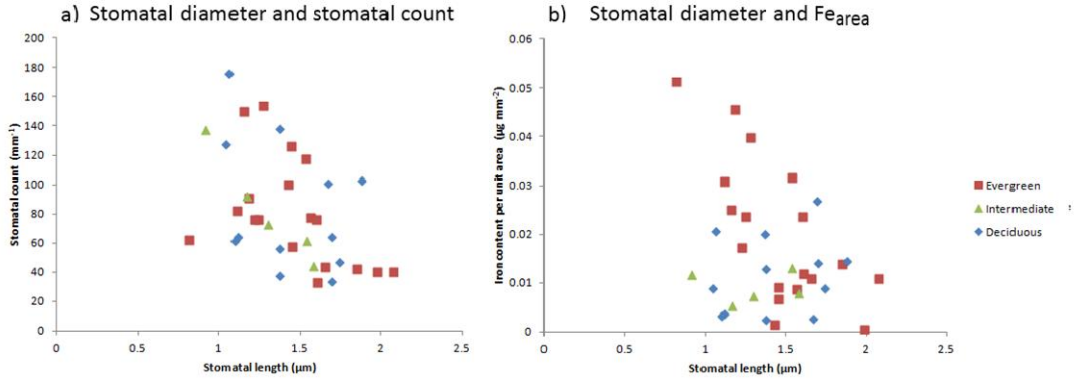


Figure 3.13: Leaf stomatal size (diameter) related to a) number of stomata per leaf unit area (stomatal count) and b) Iron content per unit area (Fe_{area}) for 54 species of tree found in the Doi Suthep-Pui National Park in northern Thailand, separated by phenological leafing strategy (evergreen, deciduous and intermediate).

In deciduous species only, stomatal count was correlated negatively with both petiole length (p=0.003, Fig. 3.14a) and blade width (p=0.003, Fig. 3.14b).

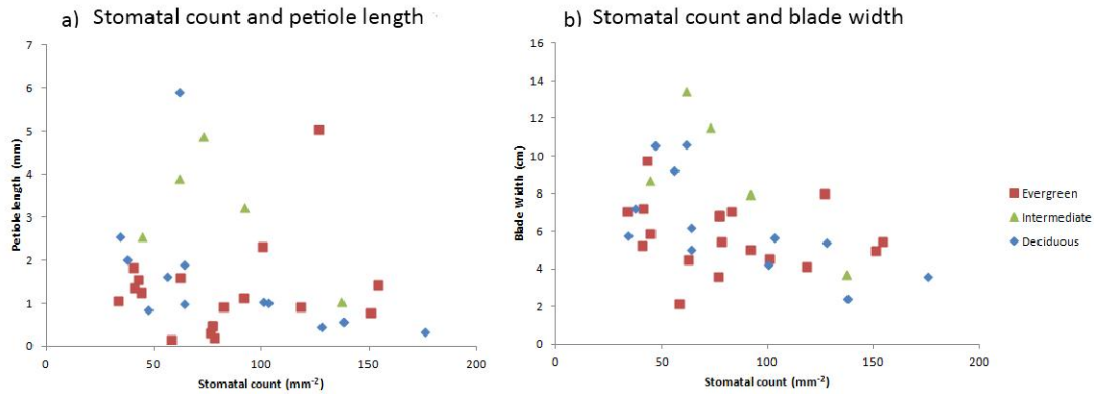


Figure 3.14: Leaf stomatal count per unit area related to a) petiole length and b) leaf blade width for 54 species of tree found in the Doi Suthep-Pui National Park in northern Thailand, separated by phenological leafing strategy (evergreen, deciduous and intermediate).

In evergreen species, the proportion of leaf surface area consisting of stomata (stomatal proportion) was correlated negatively with Ca_{mass} (p=0.007, Fig. 3.15b) Mn_{mass}, (p=0.007) and strength per unit mass (SPUM), (p=0.001, Fig. 3.15a).

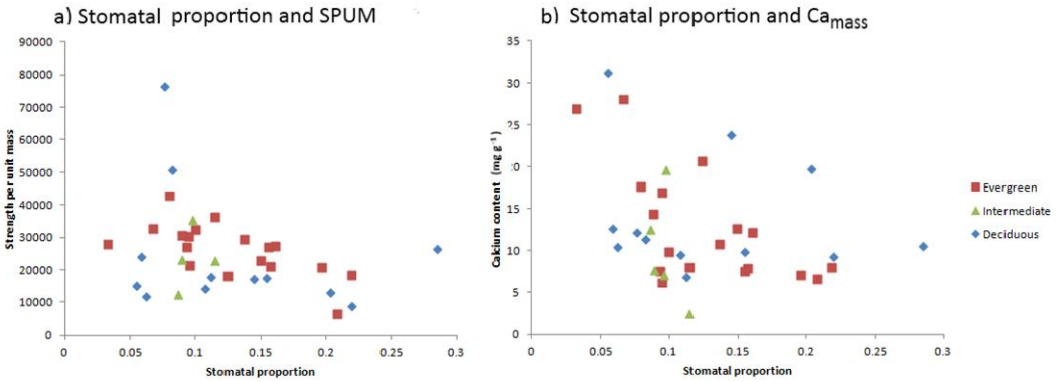


Figure 3.15: Stomatal proportion (amount of leaf surface area that consists of stomata) related to a) leaf tesile strength per unit mass (SPUM) and b) Calcium content (Ca_{mass}) for 54 species of tree found in the Doi Suthep-Pui National Park in northern Thailand, separated by phenological leafing strategy (evergreen, deciduous and intermediate).

In deciduous species, stomatal proportion was correlated negatively with K_{mass} (p=0.007,Fig. 3.16b), blade ratio (p=0.001, Fig. 3.16a) and petiole length (p=0.010).

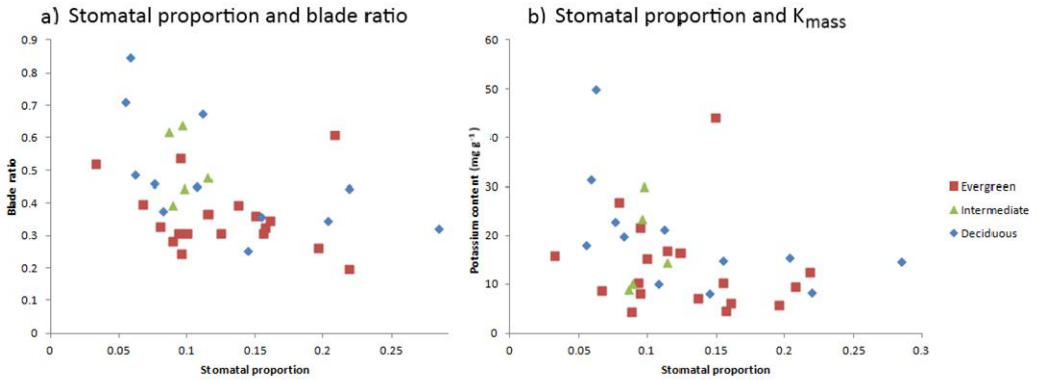


Figure 3.16: Stomatal proportion (amount of leaf surface area that consists of stomata) related to a) the ratio of leaf blade width to leaf blade length (blade ratio) and b) lead Potassium content (K_{mass}) for 54 species of tree found in the Doi Suthep-Pui National Park in northern Thailand, separated by phenological leafing strategy (evergreen, deciduous and intermediate).

3.4. Discussion

The co-ordination of leaf traits in trees from seasonally-dry tropical forests of northern Thailand was investigated. In particular, traits that have been linked previously to the avoidance and tolerance of shade, drought, herbivore damage and pathogens were analysed with reference to the leaf economic spectrum to assess whether there was evidence for the trade-off or coordination of these traits in a single axis or multiple axes of variation. Evergreen and deciduous species were compared to test the hypothesis that drought tolerance traits occur only in evergreen species for tree species found in seasonally-dry tropical forest

3.4.1. Leaf economic spectrum traits

Leaves with higher tissue density and toughness, but lower specific leaf area and nutrient concentrations are predicted to have lower photosynthetic rates, but longer life spans (Reich *et al.* 1998; Wright & Westoby 2002), i.e. a single axis of variation as described in the Leaf Economic Spectrum. Whilst photosynthetic and respiration rate were not tested here, there was evidence for the co-ordination of SLA and other traits within a Leaf Economic Spectrum; phosphate, nitrogen and SLA co-vary and 75% of variation within these three traits can be described as a single principal component. The position of leaf density on the spectrum was more complex because of the inter-relations between SLA, leaf thickness and leaf density (see below).

3.4.2. Leaf tensile strength

Leaf physical toughness has been linked to leaf life-span through both resistance to abiotic mechanical damage and because it is an effective defence against herbivores (Hanley *et al.* 2007; Onoda *et al.* 2011). Therefore, whilst it is not a classic component of the leaf economic spectrum it may be linked to the retention of biomass. Here, leaf tensile strength was considered rather than the more usual leaf compressive strength measured though a punch test. Whilst leaf breaking point was correlated with SLA, it was better described by considering lea density and leaf thickness separately. Leaf breaking point increased with leaf thickness;

however, this was not due simply to the additional tissue of thicker leaves. Instead, the thicker leaves were stronger per unit thickness. This suggests structural changes in tissue composition at higher thicknesses which suggest a larger emphasis on structural supportive tissue in thicker leaves; a concept which is intuitive and warrants further investigation. Here, whilst leaf breaking point does not differ between evergreen and deciduous species, evergreen species do have a higher Leaf Tensile Strength (LTS) which indicates that evergreen species have higher strength per unit thickness than deciduous species. This may indicate higher leaf toughness as an anti-herbivore measure against small invertebrates, where localised strength is more important than the effort required to take a bite out of an entire leaf.

3.4.3. Phenological leafing strategy (Evergreen and Deciduous)

Deciduousness is a "drought escape" adaptation to reduce water loss during drought (Levitt 1972; Singh & Singh 1992) and such species necessarily have leaves with a life-span of less than one year. As predicted due to their reduced life-span(Wright *et al.* 2004), deciduous species occur at the fast biomass gain end of the Leaf Economic Spectrum. As deciduous species avoid the drought season through leaf-drop, it might be hypothesised that they would, therefore, display fewer or reduced drought tolerance and avoidance traits than evergreen species such as thick waxy cuticles, high levels of stomatal control or trichomes. However, this was not found here. The lack of such traits in evergreen species is counter-intuitive as they retain their leaves through the hot–dry season when drought is most extreme. This could imply that evergreen species use drought tolerance methods that maintain adequate cell turgor while preventing disruptions in cellular metabolism (Munns 1988; Save *et al.* 1993) at low water levels or drought avoidance methods such as maximising water uptake through deeper root systems. They may also reduce photosynthesis during the dry season to reduce water loss, whilst still retaining their leaves. However, evergreen species exhibit may avoid drought by growing under the canopy. If this were the case, it should lead to lower survival of evergreen species when planted in open conditions, an concept that will be investigated in Chapter 8.

3.4.4. Phenological leafing strategy and leaf margin

A serrated margin has been linked to both a deciduous leaf habit and to leaf thickness. The teeth of serrated margin leaves have been found to be highly photosynthetically active, with high transpiration (Canny 1990) in young leaves early in the growing season, so accelerating growth rates relative to an equivalent un-toothed leaf (Baker-Brosh & Peet 1997; Royer & Wilf 2006) and therefore, reducing the effects of a deciduous strategy on the length of the growing season. However, this comes at the cost of higher water loss and, in drought conditions, this may outweigh the benefit of extending the growing season (Royer & Wilf 2006). In the seasonally-dry tropical forests of northern Thailand, the availability of water in the growing season is such that this would not be a concern. Alternatively, Givnish (1988; Givnish 1999) proposed that thin leaves are more likely to be toothed because, regions along the margin between major veins in thin leaves may lack sufficient structural support. Here, deciduous species were more likely to have a serrated margin and, when considered separately, deciduous species with thinner leaves were more likely to have serrated margins than deciduous species with thicker leaves. Whilst a similar pattern was observed with evergreen species for entire and slightly serrated margins, the lack of very thin evergreen leaves did not allow for comparison of very thin leaves and margin. Results here, therefore, do not support the link to a deciduous habit *per se*, but rather identify the relationship of serrated margins with deciduous species as being due to a lack of thin, evergreen leaves.

3.4.5. Time in-leaf, thickness, density and SLA

SLA can be considered a function leaf thickness and leaf density. Leaf density and thickness varied independently in previous studies (Niinemets 1999; Wilson, Thompson & Hodgson 1999; Coste *et al.* 2005). Here, specific patterns of variation were observed. In leaves thicker than 160 µm leaf thickness and density were correlated negatively. In deciduous leaves thinner than 160µm, the correlation was positive. There were too few evergreen species with thin leaves for a significant relationship). Due to the interaction between leaf thickness and density, the

relationship of time in-leaf to SLA was interesting. In thinner deciduous species, it was leaf thickness rather than SLA that was most closely correlated. Time in-leaf was also correlated with $N_{area,}$ which, if time- in-leaf is taken as an indication of leaf life-span, suggests a longer life-span for more photosynthetically active species, in contrast with predictions from the leaf economic spectrum. Due to the close correlation of SLA and leaf thickness in these species, as well as the very small number of species considered, further work may be useful to confirm these conclusions, but it is suggestive that leaf thickness rather than SLA is a more appropriate proxy for leaf life-span.

Witkowski & Lamont (1991) suggest a variety of traits linked to variation in leaf density and thickness, (such as the effects of decreased rainfall and increased light intensity on thickness) as well as mechanisms which may be relevant, (such as effect of the number of palisade layers on thickness or the effect of thicker cell walls on density). The correlation of N_{area} with both thickness and density in thin-leaved deciduous species suggest that this may be due to an increased thickness of palisade cells, which are more tightly packed than spongy mesophyll and therefore denser. However, due to the small number of species available here, further conclusions could not be reached.

The reason for the negative correlation between thickness and density in evergreen species is also unclear and requires further investigation. The observation that here, leaf breaking point varied, not primarily due to additional leaf tissue but due to differing leaf tissue composition supports this hypothesis. Leaf tensile strength (which is linked to increased lignin and therefore reduced cavitation risk), increased with leaf thickness, while leaf density decreased. Microscopic analysis of leaf sections may provide more information on the mechanisms and environmental factors affecting these relationship such as the relative fractions of different leaf tissue types and the thickness of cell and xylem walls.

3.4.6. Leaf thickness and trichomes

The relationship of trichomes with leaf thickness, density and SLA is complicated because of the inter-relations between leaf thickness, density and SLA found (see above). This also impacts on other related traits such as Leaf Breaking Point (LBP). However, the consistency found here, regardless of phenological leafing strategy, suggest that it is the correlation between leaf thickness and trichomes that is the basis for the other correlations. Here, in both evergreen and deciduous species, thicker leaves tended to be glabrous and thinner leaves were more likely to have trichomes. Glabrescent species were of a similar leaf thickness to those with trichomes at maturity. Trichomes on leaves have been described as an anti-herbivory trait through physically stopping herbivores from accessing the leaf (Moles & Westoby 2000; Agrawal & Fishbein 2006; Hanley *et al.* 2007) and an anti-drought trait (Dahlin, Brick & Ogg 1992). Thicker leaves are often related to a greater tolerance to drought through the increase in water storage capacity (Chandra *et al.* 2004); therefore the correlations between thin leaves and trichomes may represent a trade-off between two methods of drought avoidance.

3.4.7. Leaf toughness, Ca_{mass}, trichomes and Latex

Plant-pest interactions are a fundamental aspect of many proposed explanations for plant diversity and dynamics in tropical forests (Janzen 1970; Wright 2002; Leigh *et al.* 2004). Plant responses to pests vary significantly in both type and extent, with plants often exhibiting several defensive traits simultaneously (Paul & Hay 1986; Duffey & Stout 1996; Agrawal & Fishbein 2006). Some authors have found evidence for the co-ordination of anti-pathogen traits (Kursar & Coley 2003; Agrawal & Fishbein 2006), whereas other have found evidence of trade-offs between traits (Janzen 1966; Steward & Keeler 1988; Eck *et al.* 2001; Read *et al.* 2009). Still others suggest that defensive traits vary independently (Moles *et al.* 2013). Of the traits considered here (Leaf toughness, Ca_{mass}, trichomes, Latex) that have been linked to anit-herbivory and anti-pathogen functions , all except for latex have multiple functions within the leaf, which makes analysis more difficult. Here, two major relationships were found. The relationship between trichomes and SLA have

already been ascribed to a correlation with thickness (see above), leaving only the correlation between Ca_{mass} and latex.

Latex deters chewing herbivores (Agrawal & Konno 2009). Calcium is a major macro-nutrient and has many roles within the plant leaf. It is important to the structural integrity of cell walls (Demarty, Morvan & Thellier 1984) as well as maintaining membrane integrity and transport function. Calcium is also involved in stomatal control (Ward & Schroeder 1994). As it is involved in the strengthening of cells walls, it has been linked to mechanical strength and also suggested as an anti-herbivore traits, both, both due to its role in wall strength and in the form of crystals of calcium oxalate (Ward, Spiegel & Saltz 1997), which may act as irritant to herbivores. There is also evidence for the role of calcium in protecting from several fungi and bacteria (McGuire & Kelman 1984; McGuire & Kelman 1986; Olsson 1988; Bain, Millard & Perombelon 1996; Elmer, Spiers & Wood 2007). Here, the co-occurrence of high calcium concentrations and latex suggest either a coordination of anti-herbivore and anti-pathogens traits or alternatively a coordination of drought tolerance traits, anti-herbivore and anti-pathogen traits. No difference in Ca_{mass} or Latex content was found between evergreen and deciduous species and no correlation was found between Ca_{mass} and traits described in the leaf economic spectrum or those linked to either drought or shade tolerance.

3.4.8. Density and size of stomata

According to (Loranger & Shipley 2010), thicker leaves have high stomatal density. Here, no relationship between stomatal number and leaf thickness was found. High stomatal density of small stomata, is also linked to drought tolerance and avoidance (Abrams & Kubiske 1990) as this provides higher levels of stomatal control. Here, stomatal measurements and counts were not found to differ between evergreen and deciduous species or based on trichomes and margins.

No correlations between stomatal count and numbers were found with any traits drought tolerance, such as leaf SLA, cuticle thickness or water content. However, a negative correlation between stomatal count and traits linked to maximising light interception was found in evergreen species. The reasons for this are as yet unclear.

In evergreen species, stomatal proportion was negatively correlated with both SPUM and Camass, both traits associated with mechanical strength, which suggests a trade- off between high levels of transpiration and high mechanical strength. In deciduous species, the negative correlation with K_{mass} (where potassium is known to be involved in stomatal control) appear counter-intuitive and no explanation can be given at this time.

3.4.9. Conclusions

Evidence was found for the existence of the leaf economic spectrum in the leaves of the seasonally-dry forest of northern Thailand as predicted. However, it is suggested that density and thickness as independent traits may be more valuable than SLA as components of that spectrum. It is predicted that costly leaves, with high investment in mass per unit area are likely to be more effectively defended against herbivores and pathogens (Coley & Barone 1996; Agrawal & Fishbein 2006; Hanley *et al.* 2007) and therefore, have longer lifespans (Poorter & Bongers 2006). Consequently, allocation of resources to defences is predicted to be traded-off against other plant functions such as growth or reproduction (Koricheva 2002) and high levels of protection are expected at the "robust" end of the leaf Economic Spectrum. This trade-off between investment in defence and in physiological functions is known as the growth–survival or the resource availability hypothesis (Mooney & Gulmon 1982; Coley, Bryant & Chapin 1985). Here a number of functional traits previously linked to pathogen and herbivore defence were examined against functional traits from the leaf economic spectrum. However, little evidence is available here to support the co-ordination of physical robustness and protection from herbivores and pathogens. Instead, these traits appear to vary independently of each other. As predicted, deciduous species occurred far less than evergreen species at the "biomass retention" end of the leaf economic spectrum. However, the prediction that evergreen species would display more traits linked to drought tolerance and avoided was not supported. This may be due to traits other than those tested being used for this function. Nursery trials of drought tolerance may be useful in testing this theory.

4. Co-ordination of wood traits within the seasonally-dry tropical forest of northern Thailand

4.1. Introduction

4.1.1. Wood traits and their interactions

Wood performs several essential functions in woody plants (Chave *et al.* 2009; Fortunel, Fine & Baraloto 2012) including mechanical support of leaves (Rowe & Speck 2005), water transport (Meinzer, Clearwater & Goldstein 2001; Poorter *et al.* 2010) and storage of nutrients and water. As well as trade-offs between the separate functions themselves, such as between storage and strength (Poorter *et al.* 2010), trade-offs are predicted within these functions; for example the trade-off between fast growth and the creation of strong wood that will protect against physical damage (van Gelder, Poorter & Sterck 2006) or the trade-off between water transport efficiency and the risk of that transport system failing (hydraulic safety) (Baas *et al.* 2004; Maherali, Pockman & Jackson 2004; Hacke *et al.* 2006).

A single characteristic may have multiple functions, for instance, high wood density has been linked to both protection from physical damage (van Gelder, Poorter & Sterck 2006) as well as higher hydraulic safety (Hacke *et al.* 2001a; Sperry, Meinzer & McCulloh 2008). Conflicting demands, co-occurrence of these functions and trade-offs within traits have been discussed by a number of authors (Westoby & Wright 2006; Zanne *et al.* 2006; Wheeler, Baas & Rodgers 2007; Chave *et al.* 2009; Poorter *et al.* 2010).

Seasonally-dry tropical forest experiences 2–6 months of drought each year (Olivares & Medina 1992). The importance of water storage capacity, hydraulic transport efficiency and hydraulic transport safety in seasonally-dry forest is, therefore, of particular interest. Species within seasonally dry forest may be either deciduous or evergreen, with a deciduous leafing strategy thought to be a drought avoidance trait (Levitt 1972). Here wood traits from 53 species found in the seasonally-dry tropical forest of northern Thailand were considered along with maximum tree height to establish whether physical strength, water storage capacity, hydraulic efficiency and hydraulic safety co-vary or exist as separate axes of variation.

As the same functional traits may confer more than one of these features, the differences between evergreen and deciduous species were also considered. As deciduous species do not photosynthesise during the drought season, and are therefore at lower risk of drought stress, it is predicted that they will display more traits linked to water-transport efficiency and fewer linked to hydraulic safety. It is also predicted that any covariance between hydraulic safety and other protective features, such as mechanical strength, will be less than that in evergreen species.

4.1.2. Key wood traits and their predicted relationships

(a) Wood dry density

Wood dry density is a very commonly used trait by ecologists (Chave *et al.* 2009). It is a key trait associated with the Wood Economic Spectrum (Chave *et al.* 2009) which predicts that denser wood will be stronger, and have a slower growth rate than less dense wood (Enquist *et al.* 1999). High wood density has been associated with mechanical strength (van Gelder, Poorter & Sterck 2006) and higher hydraulic safety (Hacke *et al.* 2001a; Sperry 2003; Sperry, Meinzer & McCulloh 2008) as well as protection from attack by pathogens (Alvarez-Clare & Kitajima 2007) and through these mechanisms to higher survival (Kraft *et al.* 2010). Wood density has been related to conduit traits but with conflicting results (Preston, Cornwell & DeNoyer 2006; Pratt *et al.* 2007).

(b) Maximum height

The creation of long vertical stems allows woody plants to intercept more solar radiation by positioning leaves above those of shorter neighbours (Falster & Westoby 2005) but requires considerable investment in woody tissue which results in slower growth (Kraft *et al.* 2010). This investment can be reduced by having less dense wood but at the risk of vulnerability to mechanical damage. Taller trees have been associated with wider xylem vessels (Preston, Cornwell & DeNoyer 2006; Martinez-Cabrera *et al.* 2011; Fan *et al.* 2012) and it has been suggested by Chave (2009) that this is due to the higher efficiency of wider xylem vessels in providing water and nutrients at greater heights.

(c) Water storage capacity

High wood density is associated with a trade-off with wood water content, and water storage capacity (Borchert 1994). Baas *et al.* (2004) suggests two separate but correlated trade-off axes between conductive efficiency and both mechanical strength and hydraulic safety but does not consider other traits such as water storage capacity. The Wood Economic Spectrum is less developed than the Leaf Economic Spectrum but contains a similar axis of variation represented primarily by wood dry density, a feature linked to physical strength and protection from mechanical damage (Chave *et al.* 2009). However, the Wood Economic Spectrum also considers traits linked to hydraulic safety. The extent to which these axes co-vary has been explored but either no correlation was found (Wright *et al.* 2007), or a trade-off between these two forms of protective feature identified (Baraloto *et al.* 2010). The wood economic spectrum may be linked to the C-S axis of the CSR triangle theory (Thompson & Grime 1988). This axis runs from high competition, low stress environments where biomass gain is prioritised to low stress high competition environments where protection from biomass loss is prioritised.

(d) Hydraulic safety and capacity

Cavitation, the creation of gas embolisms within xylem vessels, compromise sap delivery and may cause die-back (Maherali, Pockman & Jackson 2004; Sperry 2011). Cavitation may occur in two ways, air-seeding, when gas is pulled into xylem vessels through pores in the xylem pit membrane (Sperry & Tyree 1988; Baas *et al.* 2004) and xylem implosion, where xylem conduit walls bend or collapse (Hacke *et al.* 2001b; Brodribb & Holbrook 2005). Some authors propose a trade-off between the efficiency of wider xylem vessels in sap transport and the increased risk of cavitation in wider vessels (Hacke *et al.* 2001a). Other authors find that conduit diameter and vulnerability to cavitation are not related due to the importance of xylem vessel end walls in hydraulic conductivity (Choat, Cobb & Jansen 2008). Thicker xylem vessel walls has been proposed as a mechanism for prevention of xylem implosion (Hacke *et al.* 2001a) and may, therefore, offset the vulnerability of wider xylem vessels.

4.2. Methods

4.2.1. Doi Suthep-Pui National Park

The Doi Suthep-Pui National Park (created in 1981) is an area of approximately 260 km^2 of seasonally-dry tropical forest near Chiang Mai in Northern Thailand (18.83203°N / 98.88805°E) and ranges from 340 to 1680m a.s.l (Maxwell & Elliott 2001). Whilst annual rainfall is high, rainfall between January and February can be as low as 6 mm a month, rising after the start of the monsoon in April or May to a peak of 275mm in August before dropping swiftly from October. The dry season is sub-divided into the cool-dry season (November–January) where maximum temperatures range from 30 ^{o}C to 32 ^{o}C and the hot-dry season (February– April), with a maximum daily temperature between 30 ^{o}C and 39 ^{o}C (Fig. 4.1).

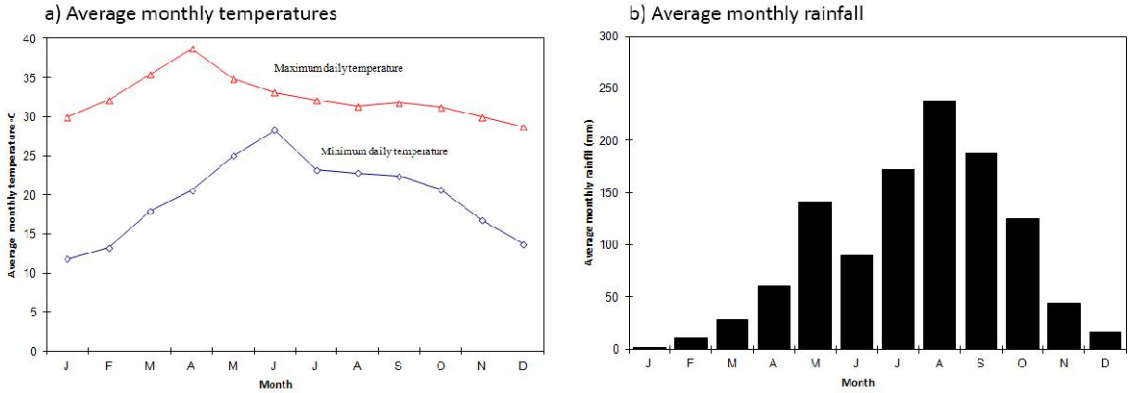


Figure 4.1: Monthly (a) maximum and minimum daily temperature and (b) rainfall in the Chiang Mai area of northern Thailand. Based on records from between 1952 and 1997– (Maxwell & Elliott 2001)

4.2.2. Species selected

Species used here consisted of 53 species planted as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand between 1998 and 2001 (Table 4.1). The species for which data have been collected covered 23 families, with many families containing only a single representative. Species were placed in four broader groups (clades). i.e. (Rosids, 35 species,; Asterids, 7 species; Eudicots, 1 species and Magnoliids 10 species using the Angiosperm phylogeny Group System 111 (Bremer *et al.* 2009).

Table 4.1: The 53 species of tree and corresponding species code and clade found in Doi Suthep-Pui National Park from which wood trait data has been collected.

Species_Name	Code	Clade	Species_Name	Code	Clade
Acrocarpus fraxinifolius	S031	Rosids	Glochidion kerrii	S179	Rosids
Aglaia lawii	S123	Rosids	Gmelina arborea	S078	Asterids
Alseodaphne andersonii	S101	Magnoliids	Helicia nilagirica	S104	Eudicots
Aphanamixis polystachya	S060	Rosids	Heynea trijuga	S157	Rosids
Balakata baccata	S015	Rosids	Horsfieldia amygdalina	S119	Magnoliids
Betula alnoides	S048	Rosids	Horsfieldia thorelii	S236	Magnoliids
Bischofia javanica	S004	Rosids	Hovenia dulcis	S018	Rosids
Callicarpa arborea	S156	Asterids	Lithocarpus elegans	S280	Rosids
Castanopsis acuminatissima	S270	Rosids	Lithocarpus fenestratus	S337	Rosids
Castanopsis calathiformis	S335	Rosids	Macaranga denticulata	S009	Rosids
Castanopsis tribuloides	S269	Rosids	Machilus bombycina	S163	Magnoliids
Cinnamomum caudatum	S207	Magnoliids	Manglietia garrettii	S007	Magnoliids
Cinnamomum iners	S218	Magnoliids	Markhamia stipulata	S204	Asterids
Diospyros glandulosa	S012	Asterids	Melia toosendan	S005	Rosids
Erythrina subumbrans	S317	Rosids	Michelia baillonii	S138	Magnoliids
Eugenia albiflora	S325	Rosids	Morus macroura	S081	Rosids
Eurya acuminata	S086	Asterids	Nyssa javanica	S146	Asterids
Ficus altissima	S072	Rosids	Phoebe cathia	S379	Magnoliids
Ficus benjamina	S029	Rosids	Phoebe lanceolata	S268	Magnoliids
Ficus glaberrima	S361	Rosids	Prunus cerasoides	S071	Rosids
Ficus heteropleura	S372	Rosids	Pterocarpus macrocarpus	S092	Rosids
Ficus hispida	S380	Rosids	Quercus semiserrata	S062	Rosids
Ficus racemosa	S365	Rosids	Rhus rhetsoides	S019	Rosids
Ficus semicordata	S315	Rosids	Sapindus rarak	S013	Rosids
Ficus subulata	S039	Rosids	Sarcosperma arboreum	S105	Asterids
Ficus superba	S368	Rosids	Spondias axillaris	S066	Rosids
Garcinia mckeaniana	S128	Rosids			

Table 4.2: Wood-trait and tree height measurements collected from 53 tree speciess planted in 1998 and 1999 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

Variable	Units	Calculated
Wood wet density	g mm^{-3}	Wet weight/Volume
Wood dry density	g mm^{-3}	Dry weight/Volume
Water content	g mm^{-3}	Wet density-Dry density
Xylem diameter	µm	Mean measurement
Xylem cross section	mm^2	$(\text{Xylem diameter}/2)^2 * p/10^6$
Xylem count	Count mm^{-2}	Count
Xylem proportion	Proportion	Xylem Count*Xylem cross section
Xylem conductivity	Relative	$(\text{Xylem diameter})/2)^4$
Wood conductivity	Relative	Xylem conductivity*Xylem Count
Xylem wall thickness	µm	Mean measurement
Fibre wall thickness	µm	Mean measurement
Total wall thickness	µm	Mean measurement
Tissue water content	g mm^{-3}	Water content – vessel water content
Mature tree height	m	Collated from literature
Clade	Category	Assigned using APG 111 system
Phenological leafing strategy	Category	Collated from literature

4.2.3. Wood Trait Collection

Wood trait data (Table 4.2) was collected during the 2011 wet season from saplings in the 1998 or 1999 plots that were not coppiced re-growth to ensure saplings of equal age. Cores were taken from trees at breast height (1.3m) using a 5.1 mm increment borer, placed immediately into plastic bags with damp tissue and processed within 24 hours. Due to the varying diameter of trees, heartwood was available only for some of the samples. All cores were trimmed to remove heartwood to remove this inconsistency. Bark and the ends levelled to create cylinders. The length of each cylinder was measured using an electronic gauge and weighed before being dried for 3 days at 70 ◦C and re-weighed.

Transverse sections of approximately 20µm thickness (up to 30µm thick in fragile specimens) were cut from wood cores with a slide microtome. Samples were taken as close to the outer cambium as possible to minimise inconsistency. These were then step-dehydrated in ethanol and stained with 1% Safranin and 1% Alcian Blue before mounting in Euparal. Transverse sections were photographed at x 50 resolution and images examined using ImageJ software to measure the diameter of a minimum of 20 xylem vessels for each species (Fig. 4.2). The values provided the xylem vessel diameter measurements. Xylem vessel counts were made on least five transverse sections per species to provide counts of xylem vessels per mm^2. Sections were observed under X400 resolution to obtain data on wood fibre wall thickness, fibre lumen size, xylem vessel wall thickness and total wall thickness (the thickness of the combined wall between the xylem lumen and the lumen of an adjoining cell).

4.2.4. Maximum tree height and phenological leafing strategy

Maximum tree height and phenological leafing strategy (deciduous, evergreen or intermediate) were extracted from a variety of published and unpublished sources including the Flora of China (Zhengyi, Raven & Deyuan 1994+), Flora of Thailand (Flora of Thailand Editorial Board 1970+) and the Chiang Mai University herbarium.

a) X50 magnification **b) X400 magnification**

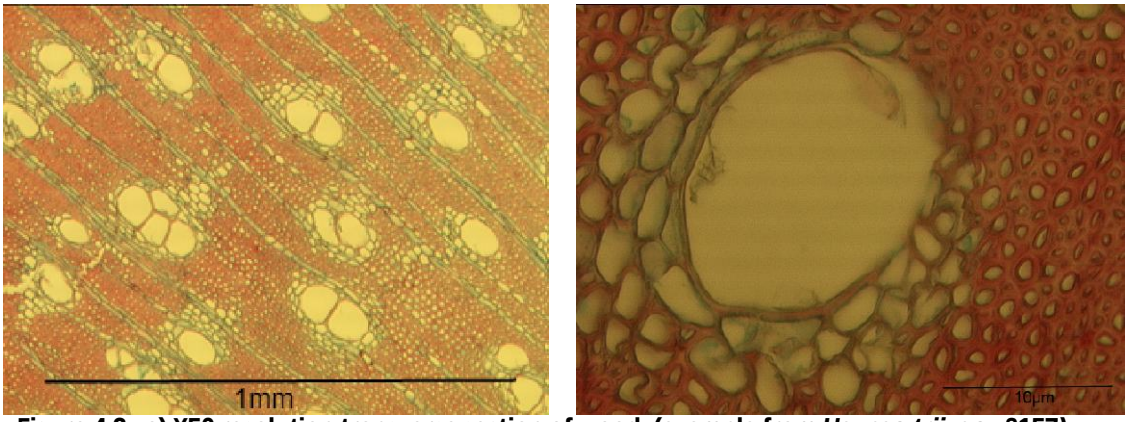


Figure 4.2: a) X50 resolution transverse section of wood, (example from *Heynea trijuga* –S157*)* suitable for counting and measuring xylem vessels and b) X400 resolution transverse section (example from *Markhamia stipulate* – S204*)* suitable for measuring wood xylem vessel and cell wall thickness.

4.2.5. Derived characteristics calculation

The relative hydraulic conductance of xylem vessels were calculated using the

$\frac{\pi r^4 P}{8 \eta l}$ (Tyree & Ewers 1991) where r = xylem radius, n = medium viscosity, P =negative pressure on the liquid and l = capillary length. This was simplified to assume standard sap viscosity, pressure and xylem vessel length (Hinckley & Zimmerman 1984) as these measurements were not available. Other constants (such as π) were removed from the equation, leaving relative hydraulic conductivity = r^4, where r is the radius of the xylem tube. The relative hydraulic conductivity of wood was calculated by multiplying the hydraulic conductance of a single xylem vessel by the number of vessels. Vulnerability to cavitation was calculated as proportional to (total vessel wall thickness/xylem lumen diameter)^2, (Hacke & Sperry 2001). For other calculations see Table 4.2.

4.2.6. Statistical analyses

Correlations between continuous traits were performed using the Pearson product-moment correlation coefficient. Where assessments were made of whether three or more samples differed significantly, the non-parametric method (Kruskal-Wallis one-way analysis method) was used, because of the highly-skewed nature of most of the continuous trait data used. Where two samples were compared, the Mann-Whitney U-test was used.

4.3. Results

4.3.1. Differences between evergreen and deciduous species and between clades

Evergreen trees were shorter than deciduous trees (p=0.023). Xylem cross-sectional area did not differ significantly between phenological leafing strategies (p=0.060), but the species with the widest xylem vessels (*Erythrina subumbrans* - S317, *Melia toosendan* - S005, *Ficus semicordata* - S315, *Prunus cerasoides* - S071, *Morus macroura* - S081) were all deciduous or intermediate (Fig. 4.3).

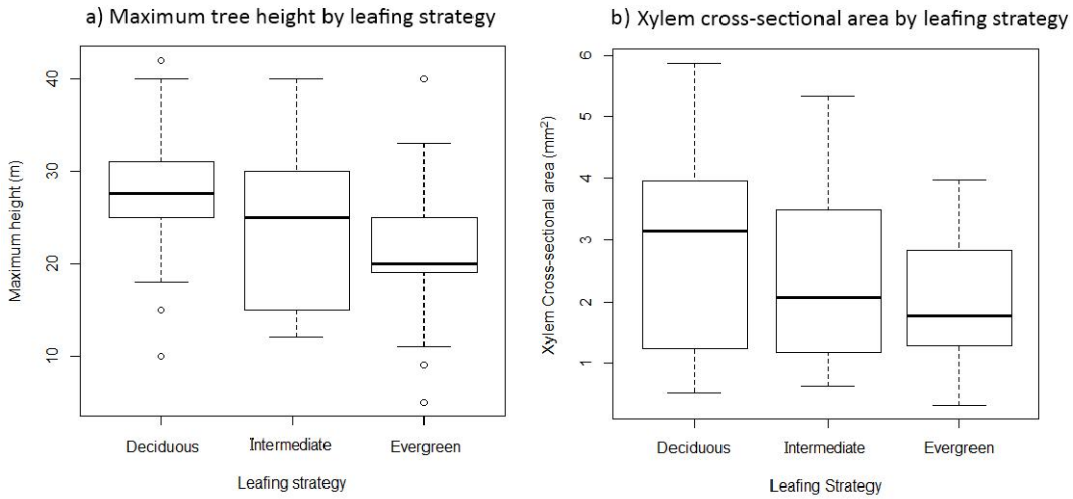
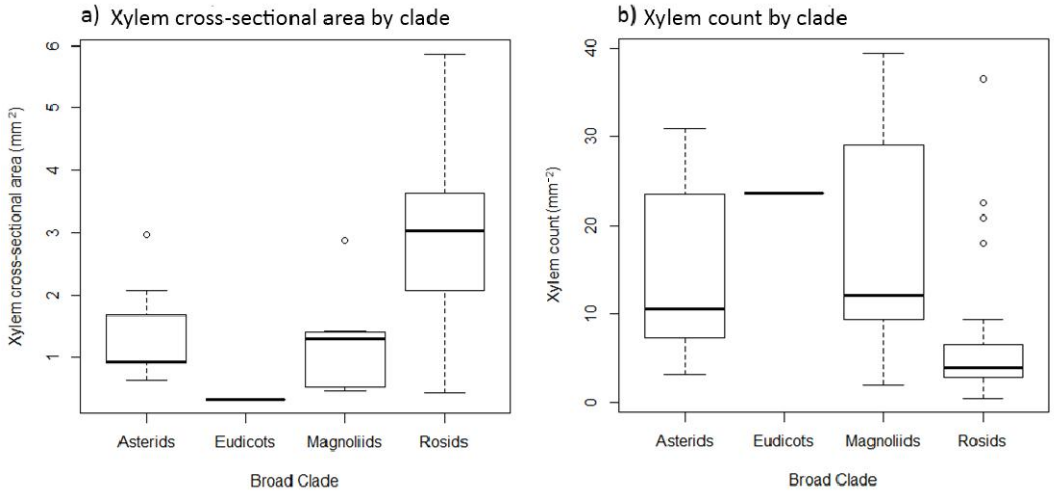


Figure 4.3: (a) Maximum height and (b), xylem cross-sectional area, of 53 tree species with different phenological leafing strategy planted within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

Rosids had fewer, but wider, xylem vessels with thicker walls than other groups (Fig. 4.4).



4.4: Xylem characteristics; (a) xylem vessel cross sectional area and (b), xylem count per mm^{-2}, within different clades of 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

4.3.2. Initial correlations between traits

Correlations were made between all traits and are discussed below in detail. Due to the small number of species (n=28 for evergreen species and n=16 for deciduous species), individual relationships were compared in graphical form to assess the likelihood of significance changes being due to reduced numbers in deciduous species (Table 4.3).

Table 4.3: Pearson correlations of wood traits for 53 species of trees seedling planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Separated by a) clade and b) leafing strategy. Deciduous species in the bottom left, Evergreen species in top right.

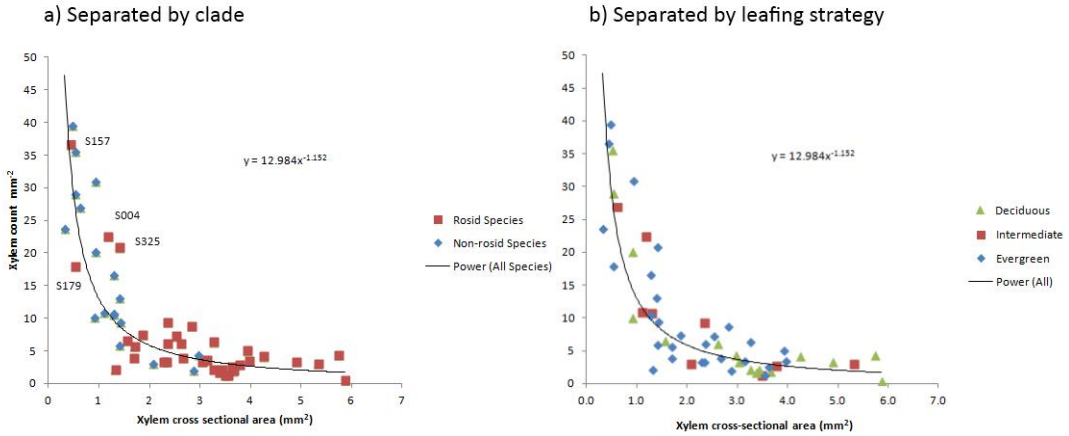
Evergreen species correlations

	dry wood density	water content	xylem diameter	xylem cross-section	xylem proportion	xylem per mm	xylem wall thickness	fibre wall thickness	full wall thickness	tissue water content	maximum Height
dry wood density		-0.077 (0.348)	-0.359* (0.030)	-0.418* (0.013)	0.071 (0.359)	0.192 (0.164)	-0.172 (0.190)	0.335* (0.04)	0.090 (0.325)	-0.103 (0.302)	0.236 (0.114)
water content	-0.028 (0.459)		0.033 (0.434)	0.063 (0.374)	-0.041 (0.419)	-0.053 (0.394)	-0.104 (0.299)	0.0507 (0.400)	0.210 (0.141)	0.816** (0.000)	-0.320* (0.048)
xylem diameter	-0.223 (0.203)	0.225 (0.201)		0.987** (0.000)	-0.081 (0.342)	-0.784** (0.000)	0.634** (<0.001)	-0.499** (0.003)	0.067 (0.367)	0.073 (0.356)	0.342* (0.037)
xylem cross-section	-0.282 (0.145)	0.167 (0.268)	0.987** (0.000)		-0.085 (0.334)	-0.723** (<0.001)	0.620** (<0.001)	-0.502** (0.003)	0.056 (0.389)	0.099 (0.308)	0.286 (0.070)
xylem proportion	0.046 (0.433)	-0.300 (0.129)	-0.160 (0.277)	-0.102 (0.354)		0.497** (0.004)	-0.084 (0.335)	0.521** (0.002)	0.012 (0.475)	-0.610** (<0.001)	-0.004 (0.491)
xylem per mm	0.003 (0.496)	-0.417 (0.054)	-0.828** (<0.001)	-0.747** (<0.001)	0.452* (0.039)		-0.513** (0.003)	0.542** (0.001)	-0.142 (0.236)	-0.330* (0.043)	-0.353* (0.033)
xylem wall thickness	0.348 (0.094)	0.370 (0.079)	0.299 (0.130)	0.305 (0.126)	-0.183 (0.248)	-0.257 (0.168)		-0.313 (0.053)	0.171 (0.192)	-0.034 (0.432)	0.304 (0.058)
fibre wall thickness	0.431* (0.047)	0.004 (0.493)	-0.254 (0.171)	-0.242 (0.182)	0.033 (0.451)	0.225 (0.201)	-0.102 (0.353)		0.343* (0.037)	-0.262 (0.089)	-0.019 (0.461)
full wall thickness	0.725** (0.001)	0.088 (0.374)	-0.058 (0.415)	-0.090 (0.370)	-0.194 (0.236)	-0.070 (0.398)	0.691** (0.002)	0.238 (0.187)		0.160 (0.208)	-0.042 (0.417)
tissue water content	-0.040 (0.442)	0.939** (0.000)	0.245 (0.180)	0.175 (0.258)	-0.610** (0.006)	-0.509* (0.022)	0.373 (0.077)	-0.008 (0.487)	0.143 (0.299)		-0.251 (0.099)
maximum Height	-0.049 (0.428)	-0.454* (0.039)	0.045 (0.434)	0.062 (0.410)	-0.122 (0.326)	0.081 (0.382)	-0.304 (0.126)	-0.241 (0.184)	-0.036 (0.448)	-0.333 (0.104)	

Deciduous species correlations

4.3.3. Xylem vessel count and xylem vessel width

Wider xylem vessels had thicker walls ($p < 0.001$) and were associated with wood fibres with thinner walls ($p = 0.003$). These correlations were significant only in evergreen species. A negative power relationship ($y = 12.984x^{-1.152}$) was observed between the cross-sectional area of xylem vessels and the number of xylem vessels within the section (Fig. 4.5). This relationship was independent of clade (Fig. 4.5a) or phenological leafing strategy (Fig. 4.5b).



4.5: Relationship between Mean Wood Xylem Vessel cross-sectional area and count of xylem vessels per mm^2 for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Separated by a) clade and b) phenological leafing strategy.

4.3.4. Xylem vessel conductance

Xylem vessel conductance was calculated from xylem diameter to correct for the decreased efficiency of narrower xylem vessels (Section 4.2.4). Xylem vessel conductance was not significantly different between evergreen and deciduous species. However, the range of values for evergreen species was far smaller than that for deciduous species ($p = 0.007$) and species with very high conductance were all deciduous species (Fig. 4.6). The differences between groups (both clade and phenological leafing strategy) were similar to, but more pronounced than those shown by xylem cross-sectional area (Fig. 4.3 and Fig. 4.4). Species with higher relative xylem vessel conductance were almost entirely limited to the Rosid group.

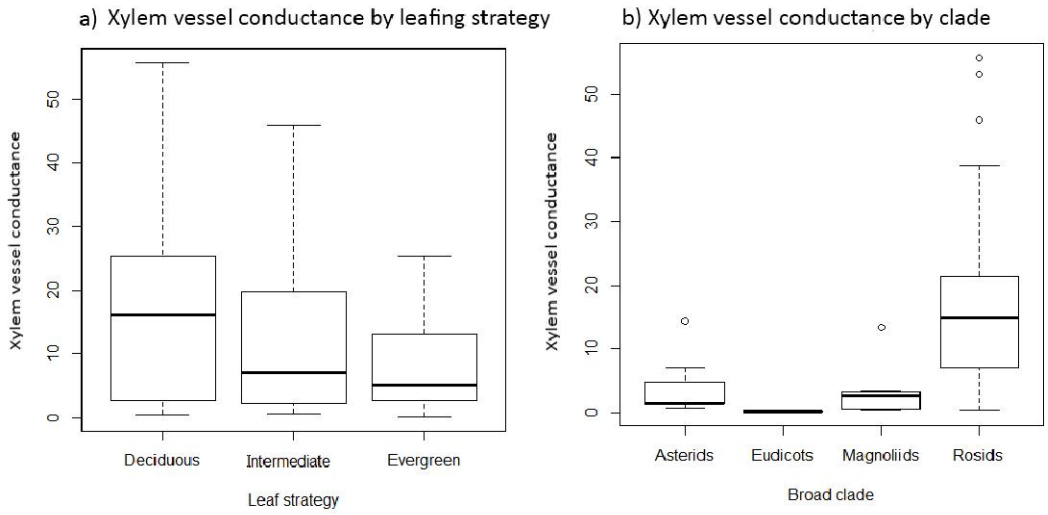


Figure 4.6: Relative xylem vessel conductance in different groups; (a) phenological leafing strategy and (b), clade, in 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

Correlations between wood traits and xylem vessel conductance were calculated and compared with those between the same traits and xylem cross-sectional area (Table 4.4). In evergreen species, xylem cross-sectional area was correlated positively with wood dry density (p=0,013) and xylem wall thickness (p <0.001) and negatively with fibre wall thickness (p=0.003), (Table 4.4). When xylem vessel conductance was considered in the place of xylem cross-sectional area, the relationship with wood dry density became slightly more significant, and the others slightly less so.

Table 4.4: Correlations between xylem cross-sectional area and xylem vessel conductance, against wood traits for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Significant correlations are marked in bold

	Evergreen correlations		Deciduous correlations	
	Xylem cross-sectional area	Xylem vessel conductance	Xylem cross – sectional area	Xylem vessel conductance
Wood dry density	**-0.418*** **(0.013)**	**-0.494**** **(0.004)**	-0.282 (0.145)	-0.365 (0.082)
Xylem count	**-0.723***** **(<0.001)**	**-0.598 ***** **(<0.001)**	**-0.747***** **(<0.001)**	**-0.598**** **(0.009)**
Xylem wall thickness	**0.620***** **(<0.001)**	**0.556*** **(0.001)**	0.305 (0.126)	0.300 (0.130)
Fibre wall thickness	**-0.502**** **(0.003)**	**-0.469**** **(0.006)**	-0.243 (0.183)	-0.211 (0.216)

The impact of considering xylem vessel conductance instead of xylem vessel cross-sectional area can be seen by comparing their relationships with cell wall thicknesses (Fig. 4.7); the spread of smaller xylem vessels was reduced, whereas the spread of narrower vessels, mainly deciduous species, was relatively broader. However, the relationships appeared similar between phenological leafing strategy groups and significance does not appear to be impinged in deciduous species by the smaller number of species available for that phenological leafing strategy.

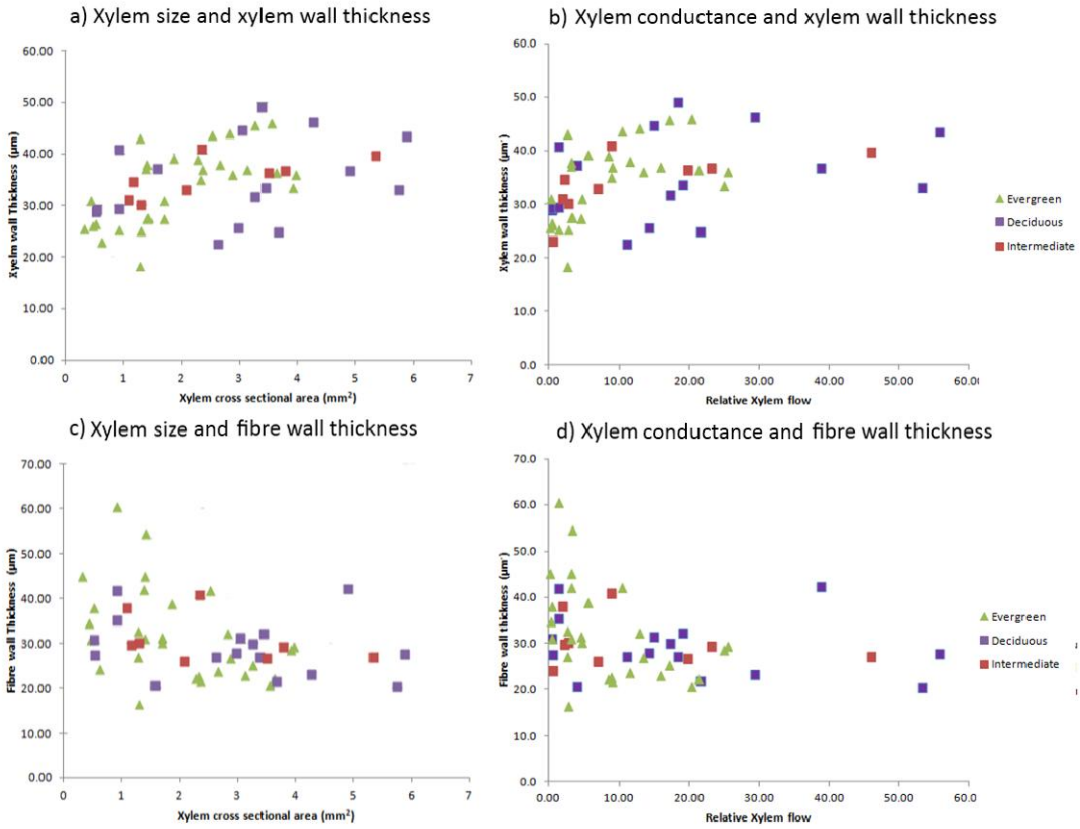


Figure 4.7: Relationship between Xylem vessel cross-sectional area (a&c) or xylem vessel conductance (b&d) and xylem wall thickness (a&b) or fibre wall thickness (c&d) for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

4.3.5. Xylem proportion and relative wood conductance

Relative wood conductance was calculated (section 4.2.4) to provide an indication of sap flow rates per mm^2 of wood. It was predicted that xylem proportion would be correlated negatively with xylem diameter and cross section but no such relationship was found. However, when relative wood conductance was used instead of xylem proportion, there was a strong positive correlation ($p<0.001$) in both evergreen and deciduous species (Fig. 4.8a, Fig. 4.8b and Table 4.5). Whilst there was no relationship between xylem proportion and xylem wall thickness, there was a positive correlation between relative wood conductance and xylem wall thickness in evergreen species. (Fig. 4.8c, Fig. 4.8d , Table 4.5). The relationships between xylem proportion and both fibre wall thickness and tissue water content did not occur when relative wood conductance was considered in its place (Fig. 4.9 and Table 4.5).

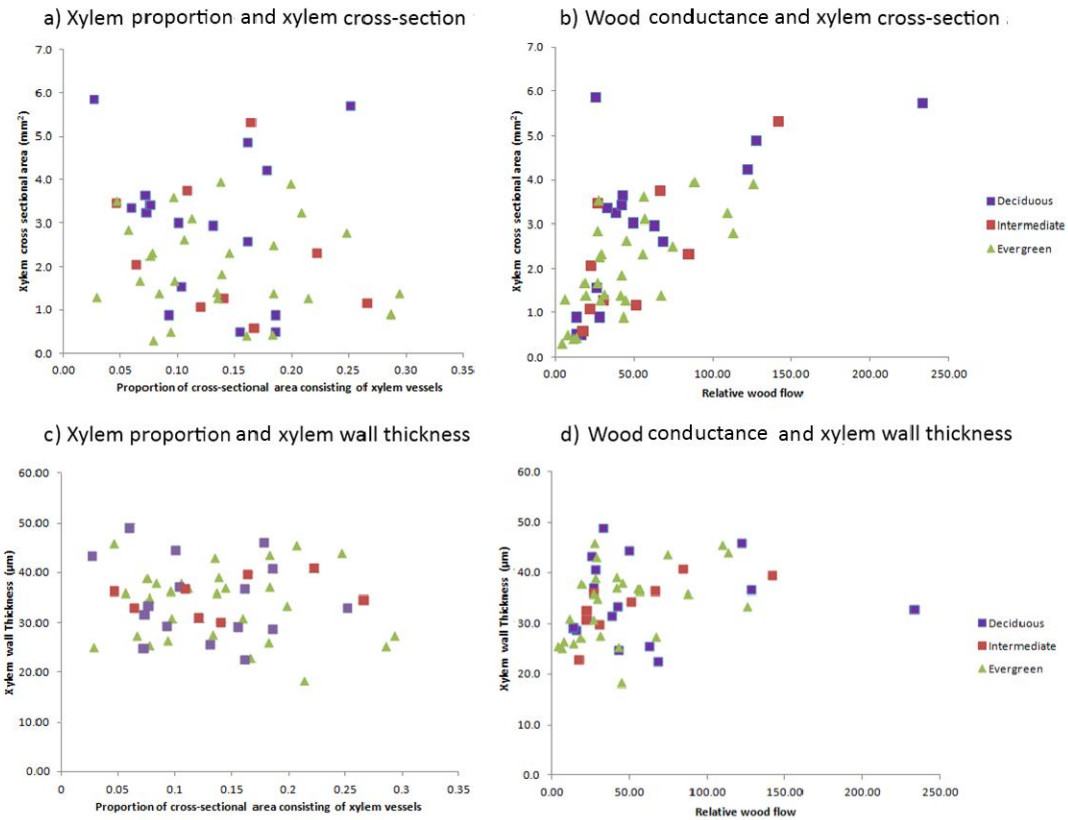


Figure 4.8: Relationship between either xylem vessel lumen area as a proportion of wood transverse sectional area (xylem proportion) (a&c) or theoretical calculated conductance of liquid per unit of wood transverse sectional area (wood conductance) (b&d) and xylem cross-sectional area (a&b) or xylem vessel wall thickness (c&d) for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

Table 4.5: Correlations between either xylem vessel lumen area as a proportion of wood transverse sectional area (xylem proportion) or theoretical calculated conductance of liquid per unit of wood transverse sectional area (relative wood conductance) and wood traits for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Significant correlations are marked in bold.

	Evergreen correlations		Deciduous correlations	
	Xylem proportion	Wood Conductance	Xylem proportion	Wood Conductance
Xylem cross section	-0.085 (0.334)	**0.692*** (<0.001)**	-0.102 (0.354)	**0.652*** (<0.001)**
Xylem wall thickness	-0.0.84 (0.335)	**0.437** (0.010)**	-0.183 (0.248)	0.057 (0.417)
Fibre wall thickness	**0.521** (0.002)**	0.055 (0.379)	0.033 (0.451)	-0.227 (0.199)
Tissue water content	**-0.610*** (<0.001)**	-0.265 (0.086)	**-0.610** (0.006)**	-0.270 (0.156)

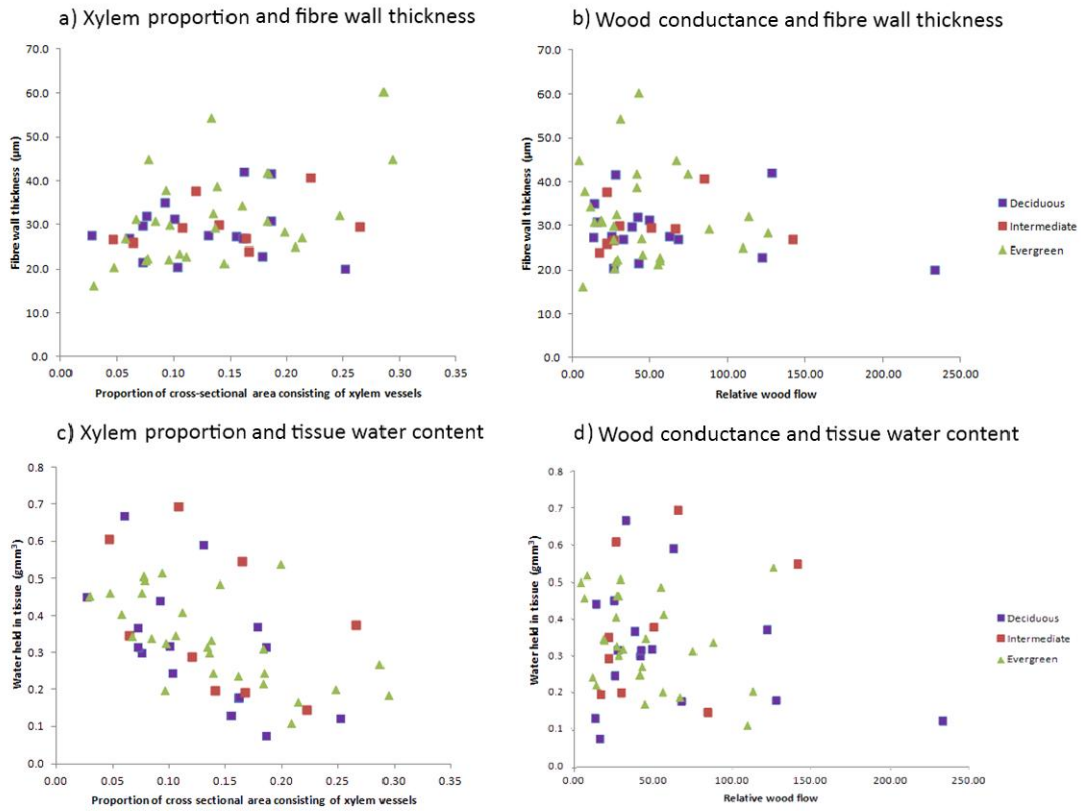


Figure 4.9: Relationship between either xylem vessel lumen area as a proportion of wood transverse sectional area (xylem proportion), (a&c) or calculated conductance of liquid per unit of wood transverse sectional area (wood conductance) (b&d) with (a&b) wood fibre wall thickness, and (c&d) wood tissue water content for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

4.3.6. Cavitation resistance

Cavitation resistance was calculated from xylem diameter and full wall thickness (section 4.2.5). Correlations of cavitation resistance generally mirrored those of xylem cross section but in the opposite direction. In evergreen species, the significance of the correlations were less with xylem wall thickness and wood conductance, similar with fibre wall thickness and more with maximum height and xylem vessel conductance. Cavitation resistance was correlated negatively with both xylem vessel conductance and wood conductance, with slightly lower significance than that with xylem cross section (Table 4.6).

Table 4.6: Correlations of xylem cross section and cavitation resistance with a number of wood traits for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Significant correlations are marked in bold

	Evergreen correlations		Deciduous correlations	
	Xylem cross section	Cavitation resistance	Xylem cross section	Cavitation resistance
Wood dry density	**-0.418*** **(0.013)**	0.090 (0.324)	-0.282 (0.145)	0.257 (0.169)
Water content	0.063 (0.374)	0.225 (0.125)	0.167 (0.268)	-0.318 (0.115)
Xylem wall thickness	**0.620*** ** **(<0.001)**	**-0.450** ** **(0.008)**	0.305 (0.126)	-0.074 (0.393)
Fibre wall thickness	**-0.502** ** **(0.003)**	**0.500** ** **(0.003)**	-0.24 (0.183)	0.326 (0.119)
Mature tree height	0.286 (0.070)	**-0.427*** **(0.012)**	0.062 (0.410)	0.029 (0.458)
Vessel conductance	**0.971*** ** **(<0.001)**	**-0.555** ** **(0.001)**	**0.963*** ** **(<0.001)**	**-0.713** ** **(0.001)**
Wood Conductance	**0.692*** ** **(<0.001)**	**-0.473** ** **(0.006)**	**0.652*** ** **(<0.001)**	**-0.508** ** **(0.022)**

4.3.7. Wood dry density

Wood dry density of evergreen species was negatively correlated with xylem diameter (p= 0.030), xylem cross-sectional area (p=0.013), and positively with fibre wall thickness (p=0.004). Within deciduous species however, the relationship was with fibre wall thickness only (p= 0.047). Wood dry density was also strongly correlated with full wall thickness but only in deciduous species (p-=0.001) (Table 4.3).

4.3.8. Wood water content

Total wood water content was correlated strongly with water held in tissue but not with that held in xylem vessels, (which is equal to xylem proportion) (Table 4.3). The water content in vessels and that in tissue were negatively correlated (evergreen $p<0.001$, deciduous $p=0.006$) (Table 4.3). Water held in tissue varied between 29% and 94% of total water in the wood. Both water in tissues and water in vessels varied significantly (tissue, 0.075 to 0.69 gmm^{-3}, xylem, 0.026 to 0.29 g $mm^{-3)}$). Water held in tissue was negatively correlated with xylem count in both deciduous ($p=0.022$) and evergreen ($p= 0.043$) species (Fig. 4.10).

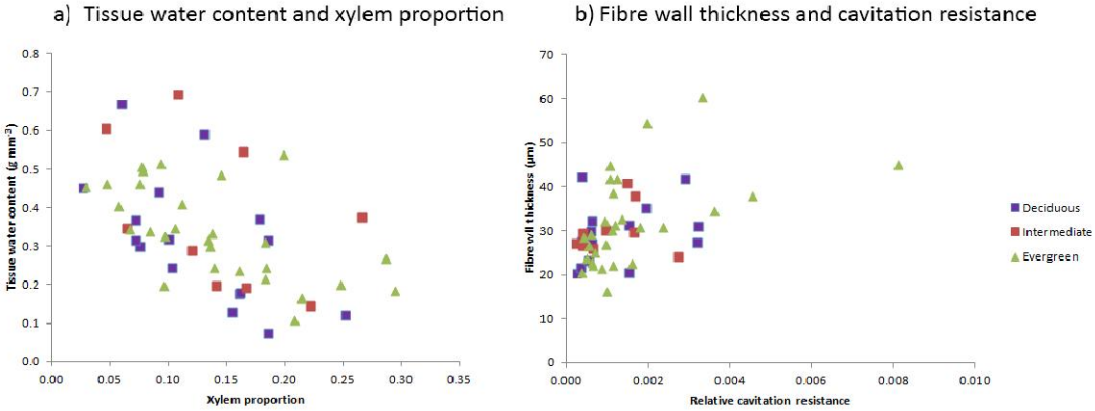


Figure 4.10: a) Wood tissue water content against xylem vessel lumen area as a proportion of wood transverse sectional area (xylem proportion) and b) wood fibre wall thickness against calculated cavitation resistance for 53 tree species planted in within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

4.3.9. Maximum mature tree height

In deciduous species, maximum mature tree height was negatively correlated with water content only ($p=0.039$). In evergreen species, maximum mature tree height was negatively correlated with water content but specifically with water held within wood tissue; it was unrelated with water held in xylem vessels (which would be proportional to xylem proportion) (Table 4.3). It was also positively correlated with vessel conductance ($p=0.018$), (Table 4.4) and negatively with wood conductance ($p=0.034$),(Table 4.4) and cavitation resistance ($p= 0.012$), (Table 4.5).

4.4. Discussion

Observed and predicted relationships were compared to assess the relative importance of wood traits in seasonally-dry tropical forest. The role of four potentially conflicting functions: (1) water transport efficiency, (2) safety from cavitation, (3) mechanical strength, and (4) water storage were considered in conjunction with phenological leafing strategy (evergreen and deciduous) and maximum height. Results were analysed to assess support for the predictions of (a) a single Wood Economic Spectrum (Chave *et al.* 2009) on which all protective features co-occur, or (b) as other authors have found, separate axes of variation for each of these traits (Maherali, Pockman & Jackson 2004; Chave *et al.* 2009).

Xylem cross-sectional area and xylem proportion affect both mechanical strength and sap flow. This can make it more difficult to identify trade-off relationships between these and other traits. To address this, two derived characteristics, (vessel conductance and wood conductance) were calculated. These derived traits account for the loss of liquid-transport efficiency in narrower vessels described by the Hagen–Poiseuille equation and are therefore more closely correlated with sap flow rates than the original traits. By looking at correlations with the original traits (Xylem cross-sectional area and xylem proportion) and comparing them to correlations with the derived measurements (Xylem conductance and wood conductance) it should be possible to differentiate between trade-off relationships with sap flow and those with mechanical strength.

Leaf drop during the dry season is a drought avoidance strategy (Levitt 1972). Whilst much work has been done on identifying leaf characteristics associated with a deciduous strategy (Givnish 2002), less has been carried out on out wood characteristics despite the role of wood traits in drought tolerance (Blackman, Brodribb & Jordan 2010). As evergreen species lose water through transpiration throughout the year, the relative importance of wood traits linked to reducing the risk of cavitation should be greater than in deciduous species, so allowing confirmation of the hydraulic safety role of traits that confer both hydraulic safety and other advantages.

4.4.1. Cavitation tolerance in evergreen and deciduous species

Thicker xylem vessel walls and reduced xylem width are associated with increased resistance to cavitation in drought conditions (Carlquist 2001; Tyree & Zimmermann 2002). This was not supported by the evidence here. The similarity in xylem width between evergreen and deciduous species may in part be due to the habitat exploited by the two different groups as evergreen species have been associated with under-story conditions and deciduous species with open conditions (see chapter 3). However, the species with the widest xylem vessels were all deciduous species, which suggests that, for species found in the canopy, a deciduous strategy is a valuable trait. Whilst here, no statistically-significant differences were found between phenological leafing strategy groups, there were differences in the relationships between these traits for evergreen and deciduous species. Evergreen species, with wider xylem had thicker xylem vessel walls, however, in deciduous species, there was no relationship between xylem vessel width and xylem vessel wall thickness. The thicker walls of wider xylem could be in part due to simple scaling, but this scaling effect would apply equally to evergreen and deciduous species and, as this was not observed, it suggests that the correlation between xylem wall thickness and xylem diameter was due to functionality within evergreen species. The prediction (Poorter *et al.* 2010) that wider xylem vessels, that are more vulnerable to cavitation will have thicker walls to provide additional protection, was supported.

4.4.2. Wood dry density

Wood dry density is a key trait associated with the Wood Economic Spectrum (Chave *et al.* 2009), which predicts that denser wood will be stronger than less dense wood and that species with denser wood will have slower growth rates. As there is no difference in the density of wood tissue itself, differences in wood density are almost exclusively due to the amount of lumen space in wood tissue, whether xylem or fibres (Gartner, Moore & Gardiner 2004). High wood density has been associated with both mechanical strength (van Gelder, Poorter & Sterck 2006) and higher hydraulic safety (Hacke *et al.* 2001a; Sperry, Meinzer & McCulloh 2008).

Whilst physical strength may be conferred through the thicker walls or smaller lumen of any wood cells, higher hydraulic safety is conferred only through xylem vessel characteristics. Wood density has been related to conduit traits, but with conflicting results (Preston, Cornwell & DeNoyer 2006; Pratt *et al.* 2007).

The correlation between fibre cell wall thickness and wood density found here is intuitive; thicker fibre walls make heavier wood. It might be expected that species with higher xylem proportion will be less dense than those with lower xylem proportion as the lumen of the xylem will create more empty space in the wood, so lowering its density. This was not found, which suggests that other wood features compensate for this difference. In evergreen species, the positive relationship between xylem proportion and fibre wall thickness and between xylem proportion and full wall thickness in deciduous species confirms this theory.

It would appear that wood dry density is related to a number of complimentary traits and that the extent to which dry density is related to each one is dependent on the other roles those traits play in the wood. This complexity may explain the variability of previous results (Preston, Cornwell & DeNoyer 2006; Pratt *et al.* 2007).

4.4.3. Wood conductance and xylem proportion

The varying proportion of wood that consists of xylem vessels (xylem proportion) affects mechanical strength, wood density and the amount of water flowing through an area of wood. As the proportion of wood transverse area that consists of xylem vessels increases, the amount of sap able to flow through a piece of wood will also increase. However, due to the decreased efficiency of smaller xylem vessels, species with smaller vessels will need a higher xylem proportion to transport the same amount of water. The relative hydraulic conductance of wood (wood conductance) corrects for this factor and is, therefore, more closely correlated with the sap flow within that wood tissue, and less related to the structural implications of xylem proportion. By comparing traits linked to xylem proportion and wood conductance rate, inferences may be drawn on the relative impact of wood sap conductance rates and mechanical strength on other traits.

Xylem proportion was not negatively correlated with xylem width, despite the known lower efficiency of narrower vessels predicting that a higher xylem proportion would be required for species with narrower vessels. The observed positive correlation between wood conductance and xylem cross section confirmed that species with wider xylem deliver more sap than those with narrower xylem, in both evergreen and deciduous species. This supports the prediction that wider xylem vessels are linked to both increased tree height (Preston, Cornwell & DeNoyer 2006) and more photosynthetically-active leaves (Santiago *et al.* 2004) both traits suggested as being related to a fast growth, low robustness strategy described within the CSR triangle (Grime 1977).

Wood conductance was negatively correlated with cavitation resistance, which supports a trade-off between hydraulic capacity and resistance to cavitation, in line with Chave *et al.* (2009) and counter to Sperry *et al.* (2008) which predicts that hydraulic capacity and resistance to cavitation should be primarily independent axes of variation.

4.4.4. Co-occurrence of hydraulic safety and mechanical strength

It is predicted that mechanical strength and hydraulic safety will co-occur, either as aspects of a single axis (Chave *et al.* 2009), or as two different but correlated axes (Baas *et al.* 2004) at the expense of traits linked to fast growth. Here, evergreen species with less-dense wood contained wider xylem vessels (both traits associated with fast growth at the expense of robustness (Chave *et al.* 2009). However, in deciduous species, where hydraulic safety is of less importance, no such relationship was found. This appears initially to support the predicted correlation.

Relative xylem hydraulic conductance (vessel conductance) was based on xylem vessel diameter corrected for the reduced efficiency of narrower vessels, and therefore, represents the amount of sap actually flowing through a vessel. It was predicted that relationships due primarily to mechanical strength would be more significant with xylem vessel size and that those linked to sap flow would be more significant with relative xylem vessel conductance. Cavitation resistance was calculated from full wall thickness and xylem vessel diameter to describe the

internal pressure resistance of individual xylem vessels. It was predicted that traits linked to hydraulic safety would be more significant with cavitation resistance than either vessel conductance or xylem cross section.

Here, a similar relationship was found between wood dry density and vessel conductance as between wood dry density and xylem proportion. However, no relationship was found between wood density and cavitation resistance. It would, therefore ,appear that the two traits of hydraulic safety and mechanical strength do not co-vary here, despite the initial conclusion and predictions (Hacke *et al.* 2001a; Sperry, Meinzer & McCulloh 2008; Chave *et al.* 2009).

4.4.5. Water content in tissues

Wood water storage capacity is a trait associated with drought avoidance (Borchert 1994). Given that samples here were collected during the rainy season it is reasonable to assume that the wood samples collected here were at full water holding capacity.

Here, tissue water content was negatively correlated with xylem proportion in both evergreen and deciduous species. The lack of a similar relationship when wood conductance was considered in the place of xylem proportion suggests a mechanical reason for this relationship rather than being due to the volume of water transported. and no evidence was found for a relationship between water tissue content and either water transport efficiency or hydraulic safety in conflict with the predictions of the wood economic spectrum (Chave *et al.* 2009).

4.4.6. Maximum height

The correlation of maximum height with xylem vessel size suggested support for the hypothesis that larger trees need wider vessels to allow sap to reach the canopy (Preston, Cornwell & DeNoyer 2006; Chave *et al.* 2009; Martinez-Cabrera *et al.* 2011; Fan *et al.* 2012). The fact that such species were deciduous supports the fact that the wider vessels put the tree at higher risk of cavitation (Poorter *et al.* 2010) and that, therefore, drought avoidance techniques (leaf drop in the dry season) were needed.

4.4.7. Conclusions

There is evidence to support a trade-off between the three potentially conflicting functions of wood, (a) water transport efficiency, (b) safety from cavitation and (c) mechanical strength in seasonally dry tropical forest. The theory that cavitation resistance is of less importance in deciduous species is supported as these trade-off relationships mainly occur only in evergreen species.

In line with other authors (reviewed in Chave *et al.* 2009) hydraulic safety and mechanical strength do not appear to co-vary, suggesting two separate axes of variation within wood traits. Additionally, water storage ability also appears to vary independently of the other protective features. Derived measurements such as wood conductance were valuable in separating the effects of traits linked to more than one function, in particular, by separating the role of xylem width as a mechanical trait from a hydraulic one. Consideration of these factors possibly sheds light on why other authors have found relationships between mechanical strength and hydraulic safety in other works. Confirmation of these theories by direct measurement of xylem vessel and wood conductance would be valuable.

Whilst Rosids tend towards larger xylem with higher xylem vessel conductance rates, there is no evidence that different clades display different relationships between functional traits as any differences in relationships may be explained purely through the position of species along the xylem width gradient.

5. The relationships between growth and survival as part of a forest restoration project in northern Thailand

5.1. Introduction

5.1.1. The trade-off between growth and survival

Identifying species that will survive well and grow effectively in forest restoration schemes often requires extensive field trials. Examples of such nursery and field trials aimed to develop a reforestation scheme in the Doi Suthep-Pui National Park have been run by the Forest Restoration Research Unit (FORRU) of Chiang Mai University since 1997 (Elliott *et al.* 2002; Elliott *et al.* 2003). The methods developed by FORRU, based around the Framework Species Approach to forest restoration (Goosem & Tucker 1995) have been very successful. However, these trials are time-consuming and expensive and performance data are usually not available for several years after planting (Elliott *et al.* 2002; Elliott *et al.* 2003). Additionally, new trials are required for each new ecosystem or set of available species and results vary due to uncontrollable environmental conditions, such as rainfall, for each trial. If researchers were able to predict the results of trials and anticipate how performance was likely to vary in response to environmental factors, it would reduce the need for trials and make it easier to extrapolate results to predict performance in other geographical areas as well as allow appropriate site management in the face of stochastic events or limiting factors.

The type and impact of limiting factors differs between habitats, but within the seasonally- dry tropical forest of the northern Thailand, variation in rainfall is of particular importance with the annual drought season being an important driver of diversity, species strategy and primary productivity (Murphy & Lugo 1986). Increasingly, the role of pathogens and herbivores has been recognised as important drivers, with rainfall linked to increased pathogen load (Swinfield *et al.* 2012).

5.1.2. Relationship between growth and survival – The CSR model

The CSR triangle (Grime 1977) considers the relationship between growth and survival. The CS axis of variation in the CSR triangle, which is similar to that described as the growth and survival trade-off hypothesis (Kobe *et al.* 1995) consists of a trade-off between (1) fast opportunist growth, which maximises potential biomass gains but also the risk of biomass loss and (2) growth which is slower and less competitive but exposes the plant to lower risks of biomass loss.

In environments with few limiting factors, species towards the fast growth/high risk end of this axis will out-perform those at the slow growth/low risk end (Fig. 5.1). However, in harsher conditions this potential for faster growth is at the expense of enhanced mortality. In difficult conditions, growth will be compromised and both low survival and slow growth will be observed. The CSR model also has a second axis of variation, between competition and competitor avoidance. At one end of this axis are the competitor species, with high phenotypic plasticity, which invest in a suite of competitive traits, and at the other, two groups of competitor avoiders with low phenotypic plasticity that either avoid competitors temporally, by growing and reproducing very quickly (ruderal species), or those that avoid competition geographically, by tolerating low resource environments (stress tolerators). Species with high phenotypic plasticity may exhibit fast growth or slow growth, depending on environmental factors, but will display high survival in all environments.

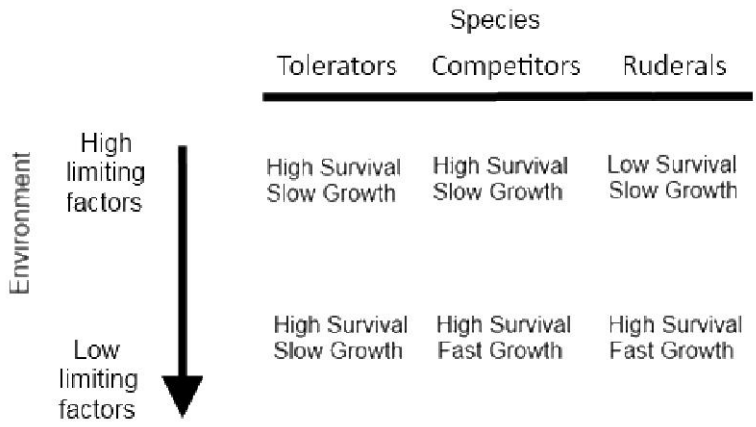


Figure 5.1: Theoretical model indicating survival and growth measures in species categories derived from the CSR model.

5.1.3. Adaptations to specific limiting factors

Whilst the growth-survival and CSR model hypotheses describe plant responses to limiting factors, they do not take account of adaptations to specific environments. In the seasonally dry forests of northern Thailand, the stresses encountered in gaps are different to those encountered in established forest. The pioneer concept describes a suite of traits linked to early successional species that convey both fast growth and high survival in open conditions. It might, therefore, be predicted that pioneer species would have high performance in a restoration site and that, counter to the predictions of the growth-survival and CSR hypotheses, survival would be correlated with growth rate. However, pioneer species are hypothesised to prioritise fast growth over tolerance traits (Swaine & Whitmore 1988; Bazzaz 1991; Whitmore 1998) and pioneer species with fast growth may therefore be more vulnerable to seedling death in sub-optimal conditions such as high pathogen loads.

At the other end of the spectrum are slow growing species which prioritise survival and prevention of biomass loss under sub-optimal conditions. However, slow growth has been linked to shade tolerating species (Blundell & Peart 2001), which are adapted for later successional conditions under the canopy and, may therefore, be predicted to have poorer performance in the open conditions of a restoration site.

No species with high shade and high drought tolerance were found in a recent review (Niinemets & Valladares 2006). However, species that germinate in the under-storey and respond to high light availability in forest gaps by quickly growing to reach the canopy are known in seasonally-dry tropical forest (Murphy & Lugo 1986). Whilst the conditions within forest gaps are not likely to be as extreme as those in open areas (Asbjornsen *et al.* 2004) such a species would need to combine tolerance for both canopy and under-canopy conditions. The extent to which general tolerance characteristics, specific adaptations and phenotypic plasticity affect species performance in response to varying environmental conditions is therefore of interest.

5.1.4. Aims and Hypotheses

The relationships between growth, survival and annual differences in rainfall pattern have been considered here in an attempt to understand performance in the field of 54 species of tree planted as seedlings in the Doi Suthep-Pui National Park as part of a restoration project from 1998 to 2001. Performance has been considered in relation to the growth-survival trade-off concept (Kobe *et al.* 1995), the CSR model (Grime 1977), the pioneer concept (Swaine & Whitmore 1988; Bazzaz 1991; Whitmore 1998)and hypotheses relating to shade tolerance (Smith & Huston 1989; Abrams 1994; Abrams & Kubiske 1994; Kubiske, Abrams & Mostoller 1996; Niinemets, Kull & Tenhunen 1998).

Hypotheses that support the growth-survival trade-off hypothesis;

- Species with fastest growth have lowest survival which varies considerably by plot.

Hypotheses that support the CSR model;

- Stress tolerators - Species with slow growth in all plots (regardless of weather conditions) have high survival in all years.
- Ruderal species – Species with fast growth in all plots have low but variable survival rates
- Competative species. Species with high survival in all plots have variable growth rates.

Hypotheses that support the concepts of drought tolerant pioneer species and shade tolerant later-succession species;

- Species with fast growth will have low survival in wet years and high survival in dry years
- Species with slow growth will have high survival in wet years and low survival in dry years

Additionally, the relationships between growth in the nursery and in the field during the first and second year after planting was investigated to see whether growth rates in the nursery be used to predict growth in the field.

5.2. Methods

5.2.1. Germination trials ((FORRU) 1998; (FORRU) 2000)

Species were grown in local nurseries to planting-out height of approximately 30-60 cm tall. Time in the nursery varied considerably between species; from a few months to 3 years depending on germination time and growth rate. Unfortunately, growth rates in the nursery were not recorded during the germination trials for all species, but here this has been estimated from mean germination time, time in the nursery and height or RCD measured two weeks after planting. Nursery growth rates are not available for each year's planting individually

5.2.2. Field plots in Doi Suthep-Pui National Park (Elliott & Anusarnsunthorn 2001; Anasarnsunthorn & Elliott 2004)

Field plots were established by FORRU in the north of Doi Suthep-Pui National Park in 1997 (Elliott *et al.* 2002; Elliott *et al.* 2003). The park (created in 1981) consists of 260 km^2 near Chiang Mai in Northern Thailand (18.83203°N / 98.88805°E) and ranges from 340 to 1680m a.s.l (Maxwell & Elliott 2001). It was initially covered with seasonally-dry tropical forest, ranging from from deciduous forest at low elevations to evergreen at higher elevations or near to water sources. The park is now only 10% forested after the loss of forest to agriculture and forest fires.

The field plots were established in a degraded watershed (18.866667°N, 94.85°E), 1,207-1,310 m above sea level. Originally, the study site had been covered with evergreen hill forest, cleared approximately 20 years previously, to provide land for cultivation and then abandoned (Elliott *et al.* 2002). Fire was used to clear stubble on a yearly basis. The data presented in this paper was derived from seedlings planted in 1998, 1999, 2000 and 2001 in the "framework" plots. In each year, three replicate formwork plots were planted (Fig 5.2). Results from each replicate site were compared (ANOVA) and found not to be significantly different from each other. However, detailed site characteristics (such as soil characteristics) for individual plots were not taken before planting.

Whilst treatments varied between years, there was a control plot and standard "framework" plot, which was prepared exactly as recommended within the original report by Goosem & Tucker (1995). Only species planted in the "Framework" plots, and therefore, treated with the same regimes during each year are included here to minimize external effects. Framework plots were planted in June to allow maximum growth before the onset of the dry season. About three weeks before planting, plots were sprayed with glyphosate, to kill weed roots and prevent immediate re-growth. Saplings were then planted randomly at a density of 3125 ha^{-1}, with 29 or 30 species planted in each plot. One hundred grams of fertiliser (NPK 15–15–15, Rabbit Brand) was added to the bottom of each planting hole immediately prior to planting. Weeding with hand tools was then carried out three times during the rainy season at 4–6 week intervals. Immediately after weeding, further 100 g doses of fertiliser were applied to each tree. For full methodological details see Elliot (2002).

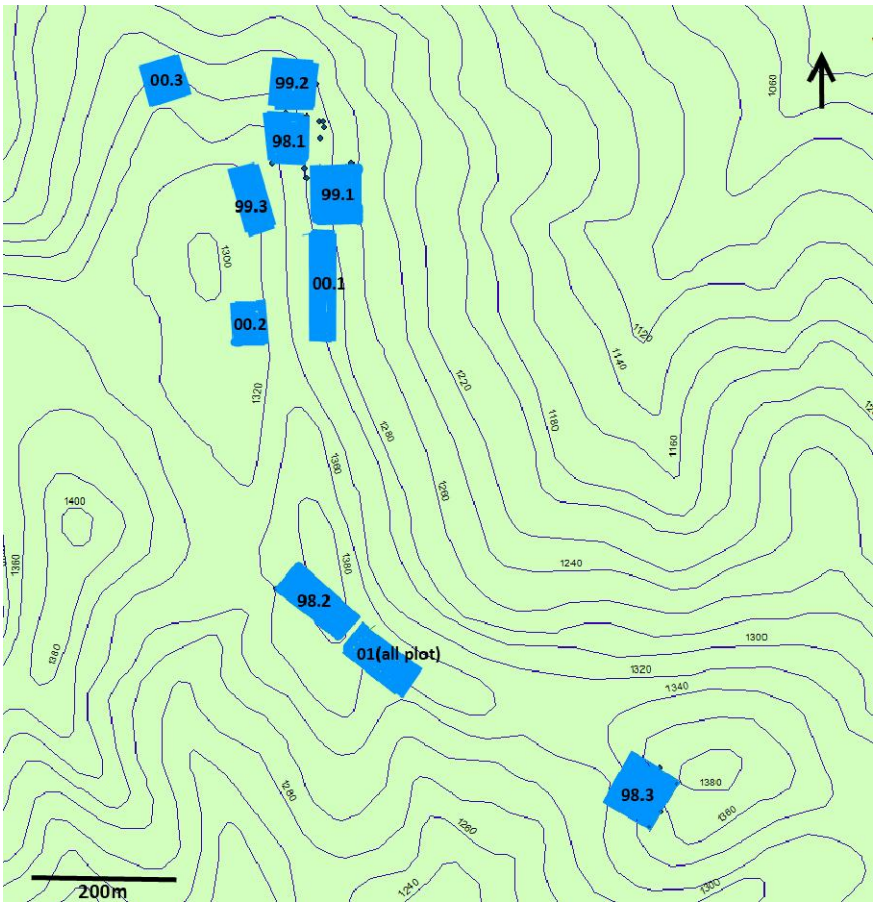


Figure 5: Map of restoration plots planted between 1998 and 2001 in Doi Suthep-Pui National Park in northern Thailand.

5.2.3. Doi Suthep-Pui National Park weather

Whilst annual rainfall is high in Doi Suthep-Pui National Park, rainfall in January and February can be as low as 6 mm a month, briefly rising at the start of the monsoon in April or May, before a slight drop in June, rising again to a peak of 275mm in August before dropping swiftly from October. The dry season is sub-divided into the cool-dry season (November–January) where maximum temperatures range from 30 ^{o}C to 32 ^{o}C and the hot-dry season (February– April), with a maximum daily temperature of between 30 ^{o}C and 39 ^{o}C (Fig 5.3).

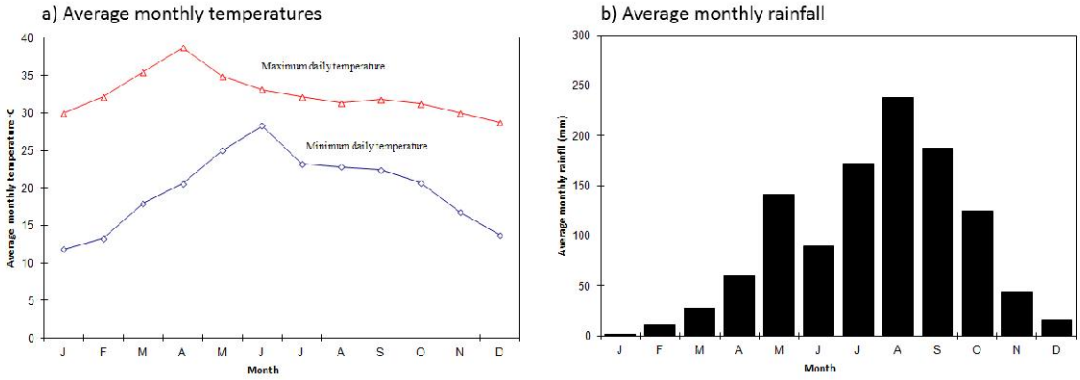


Figure 5.3: Monthly (a) maximum and minimum daily temperature and (b) rainfall in the Chiang Mai area of northern Thailand. Based on records from between 1952 and 1997– (Maxwell & Elliott 2001)

All years in the study period followed similar patterns of mean temperature, ranging from a peak in April of between 26 and 30°C, falling slightly in May and maintaining a plateau till October, when temperatures dropped again, to a low of 20 to 22°C in December and January, before rising again to the higher temperatures of May. Rainfall patterns however, varied significantly between the years in the study (Fig. 5.4).

In 1998 (Fig. 5.4a), the peak in rainfall in May was as expected but rainfall later in the wet season was slightly lower than average. The drop in rainfall between these peaks was particularly marked. In 1999 (Fig 5.4b), after a very rainy May, the period from June to September experienced lower rainfall than usual. In 2000 (Fig 5.4c), a high early peak led to a large drop in July and a reduced and delayed later rainy season. The late rainy season in 2001 (Fig 5.4d) was particularly wet and there was not a large drop in rainfall between the first and second peak. Both the early and late peak of rainfall were high in 2002 (Fig 5.4e), though the drop between them in July was severe. Finally, the drop after the initial rain May in 2003 was severe, and the second peak was very wet but brief (Figure 5.4f), (Information Services - Thai Meteorological Office-personal communication 2013).

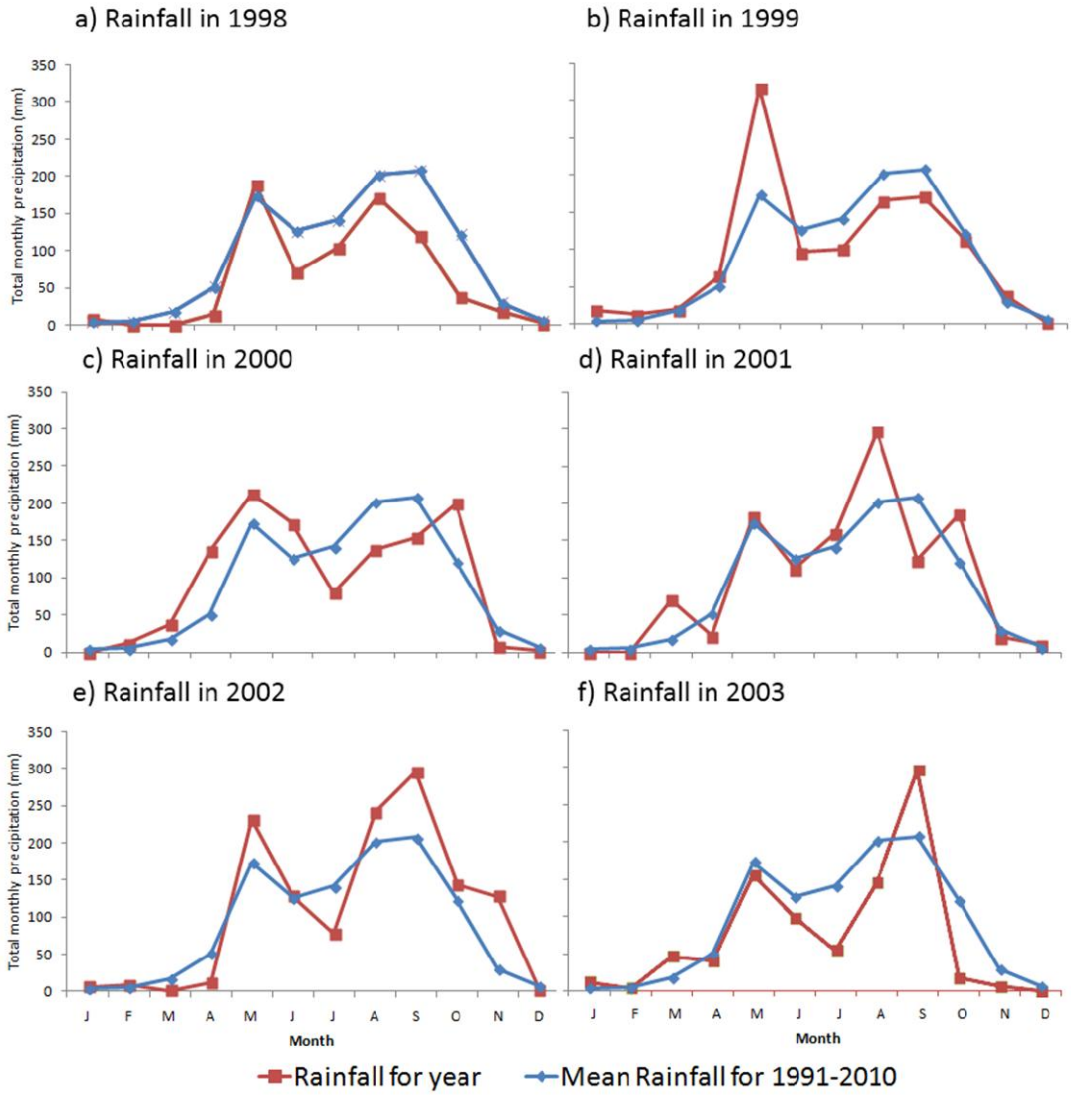


Figure 5.4: Mean monthly rainfall by month for 1998 to 2002 in Chiang Mai, Northern Thailand. (NCAS British Atmospheric Data Centre 2012)

5.2.4. Field trials – Species selection

The planting of seedlings in the field was timed for late June to early July, so providing well- watered soil, and yet several more months of rainy season to give seedlings their best chance of establishment (Elliott *et al.* 2003). Approximately 30 species were planted each year. A combination of pioneer and climax species was planted and attempts were made to ensure a good range of species in both growth-rate and habit to encourage a varied natural architecture. Many species were included in more than one year, with seven species being planted in all years (Table 5.1)

Table 5.1: Species of seedling planted in 1998, 1999, 2000 and 2001 as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand. Species code provided in brackets

	Planted in each year					Planted in each year			
Species	**98**	***99***	**00**	**01**	***Species***	**98**	***99***	**00**	**01**
Bischofia javanica (S004)	ü			ü	*Garcinia mckeaniana (S128)*	ü			
Melia toosendan (S005)	ü	ü		ü	*Michelia baillonii (S138)*		ü		ü
Manglietia garrettii (S007)	ü			ü	*Nyssa javanica (S146)*	ü	ü	ü	ü
Macaranga denticulata (S009)		ü	ü		*Callicarpa arborea (S156)*		ü		
Diospyros glandulosa (S012)	ü				*Heynea trijuga (S157)*	ü	ü	ü	ü
Sapindus rarak (S013)	ü	ü	ü	ü	*Machilus bombycina (S163)*		ü	ü	
Balakata baccata (S015)		ü	ü		*Glochidion kerrii (S179)*		ü		
Hovenia dulcis (S018)	ü	ü	ü	ü	*Markhamia stipulata (S204)*	ü		ü	
Rhus rhetsoides (S019)		ü	ü	ü	*Cinnamomum caudatum (S207)*		ü		ü
Ficus benjamina (S029)		ü	ü	ü	*Cinnamomum iners (S218)*	ü			
Acrocarpus fraxinifolius (S031)		ü			*Horsfieldia thorelii (S236)*	ü	ü		
Ficus subulata (S039)		ü	ü	ü	*Phoebe lanceolata (S268)*	ü			
Betula alnoides (S048)			ü	ü	*Castanopsis tribuloides (S269)*			ü	
Aphanamixis polystachya (S060)	ü				*Castanopsis acuminatissima (S270)*		ü	ü	ü
Quercus semiserrata (S062)	ü	ü	ü	ü	*Lithocarpus elegans (S280)*			ü	ü
Spondias axillaris (S066)	ü			ü	*Ficus semicordata (S315)*			ü	
Prunus cerasoides (S071)	ü	ü	ü		*Erythrina subumbrans (S317)*	ü	ü	ü	ü
Ficus altissima (S072)	ü		ü	ü	*Eugenia albiflora (S325)*	ü			ü
Gmelina arborea (S078)	ü	ü	ü		*Castanopsis calathiformis (S335)*	ü			
Morus macroura (S081)			ü		*Lithocarpus fenestratus (S337)*		ü		
Eurya acuminata (S086)	ü				*Ficus glaberrima (S361)*		ü	ü	ü
Pterocarpus macrocarpus (S092)		ü			*Ficus racemosa (S365)*		ü	ü	ü
Alseodaphne andersonii (S101)	ü				*Ficus superba (S368)*			ü	
Helicia nilagirica (S104)	ü		ü	ü	*Ficus abellii (S370)*			ü	
Sarcosperma arboreum (S105)	ü			ü	*Ficus heteropleura (S372)*		ü		
Horsfieldia amygdalina (S119)	ü	ü			*Phoebe cathia (S379)*		ü		
Aglaia lawii (S123)	ü				*Ficus hispida (S380)*		ü		

5.2.5. Field Monitoring

Saplings were monitored for survival and height two weeks after planting in order to assess transplantation survival and provide initial field height measurements. Monitoring was repeated in November of the planting year (+ five months after planting) to assess survival and growth after a single growing season and a final measurement was made in November of the year after planting (+ 17 months after planting) to assess the survival and growth after two growing seasons. Root Collar Diameter was measured twice (two weeks and 17 months after planting) and canopy width was measured once (17 months after planting). Growth and survival were calculated and included in the analysis (Table 5.2).

Table 5.2: Measures of growth and survival for species of tree found in Doi Suthep-Pui National Park and included in germination and growth trials by the Forest Restoration Research Unit.

Measurement	Code	Units	Calculation
Nursery Height growth rate	NGRH	Cm/days	Height1/Nursery growing time
Survival 12	S12	Percentage	Survival at 5 months / Survival at 2 weeks*100
Survival 23	S23		Survival at 17 months / Survival at 5 months*100
Survival 13	S13		Survival at 17 months / Survival at 2 weeks*100
Growth Height12	GH12	Cm	Height at 5 months – Height at planting
Growth Height23	GH23		Height at 17 months – Height at 5 months
Growth Height13	GH13		Height at 17 months – Height at planting

5.2.6. Statistical analysis

Correlations were performed using a Spearman rank correlation coefficient because the data were not normally distributed (highly skewed and presence of some outliers for most traits).

Where assessments were made of whether three or more samples differed significantly, the non-parametric method (Kruskal-Wallis one-way analysis method) was used, because of the highly-skewed nature of most of the continuous trait data used. Where two samples were compared, the Mann-Whitney U-test was used.

5.3. Results

5.3.1. Nursery Growth Results

Species planted in each plot had similar growth rates in the nursery (Fig. 5.5a) (P>0.005) and covered a similar range of growth rates (P>0.005). The distribution of growth was skewed towards slower-growing species, with only a small number of fast-growing species. Fast growing species in the nursery were *Hovenia dulcis* (S018) and *Prunus cerasoides* (S071). Height at planting out varied slightly between years, but only significantly for height between 1998 and 2001 (P<0.005), (Fig 5.5b.). Differences in ranges were not significant (P>0.005). There was a single outlier, *Hovenia dulcis* (S018, 2001 plot only).

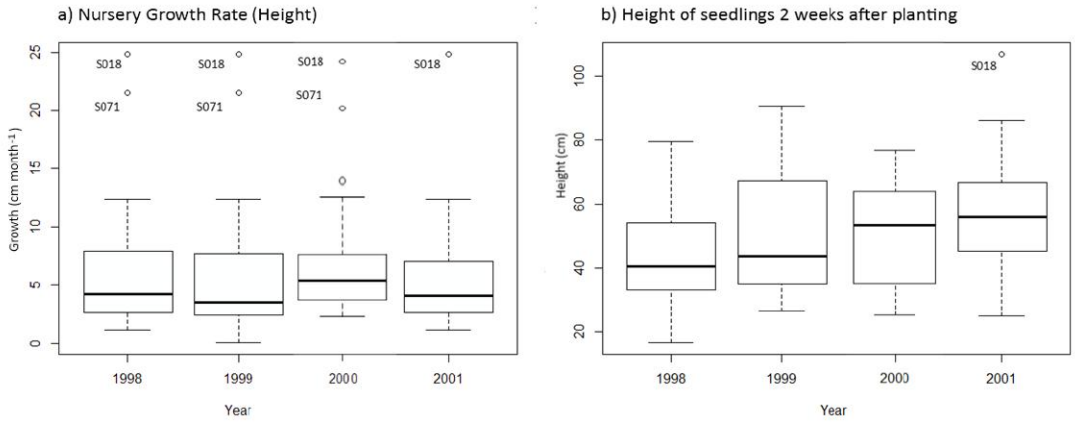


Figure 5.5: a) Nursery growth rates and b) height two weeks after planting for species of saplings planted in 1998, 1999, 2000 and 2001 in a forest restoration plots in Doi Suthep-Pui National Park.

Melia toosenden (S005) was an outlier with very high levels of growth in the 1998 and 1999 plots (1998 first season growth = 68cm, second season growth = 394cm; 1999 first season growth = 105 cm, second season growth = 556 cm),(Fig 5.7) skewing results in the years that it was planted. It has therefore not been included within the analysis for field performance.

5.3.2. Field performance

Growth rates varied; some seedlings grew only a few cm over two years in the field and others up to 2.5m. Seedlings grew faster in the 2000 plots than other years. ($P<0.05$), (Fig. 5.6a) and there were fewer very fast growing species in the 2001 plot. Survival in the 1999 plots was low (37%), compared to other years (1998 = 68%, 2000 =56%, 2001 = 57%), (Fig.5.6b)

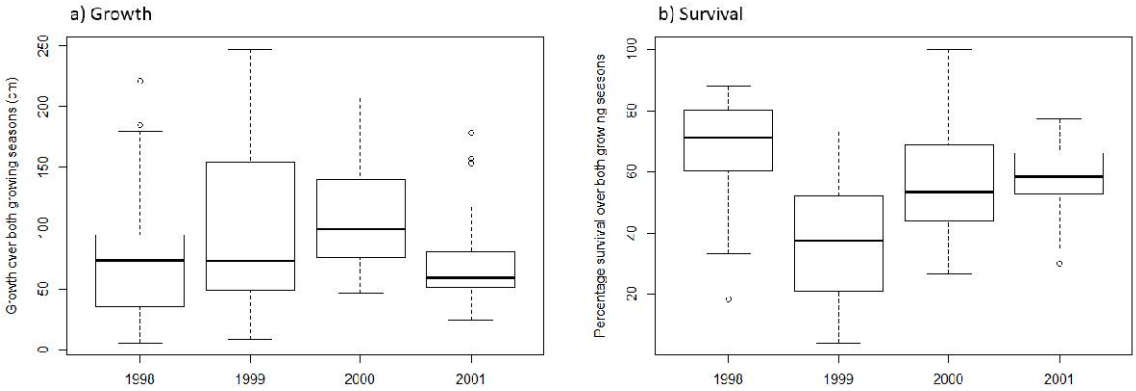


Figure 5.6: Growth and survival over the first two seasons in the field for 53 species of tree planted in Doi Suthep-Pui National Park between 1998 and 2001 as part of a restoration project.

Survival and growth were correlated positively in the 1998 ($p=0.005$), 1999 ($p= 0.006$) and 2001 plots ($p= 0.032$) but not the 2000 plot (Fig.5.7).

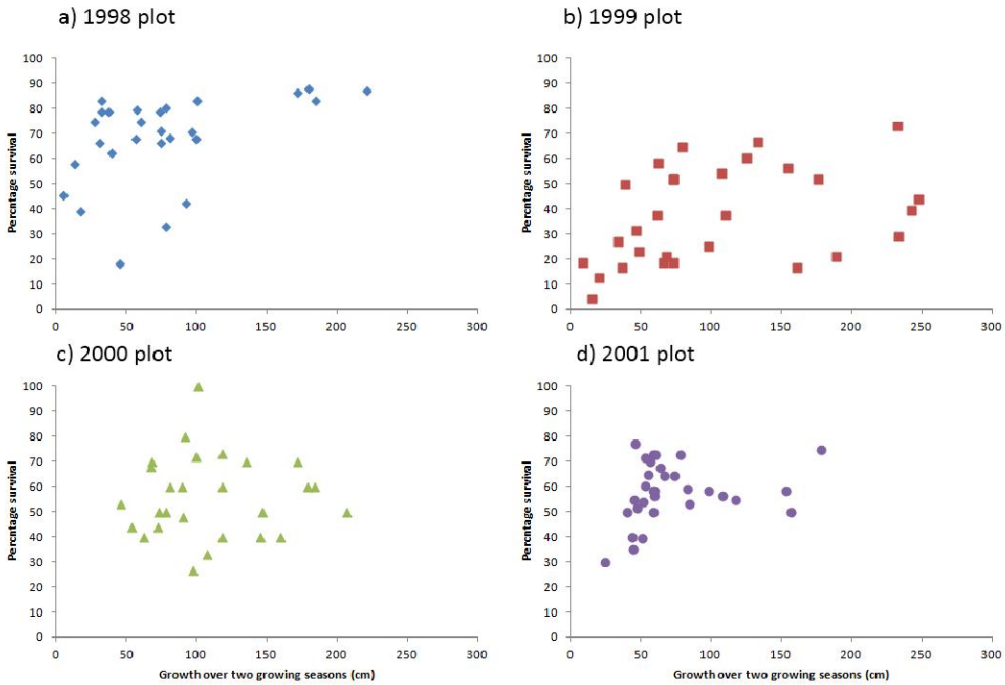


Figure 5.7: Correlation between survival and growth over first two seasons in the field for 53 species of tree planted in Doi Suthep-Pui National Park in 1998, 1999, 2000 and 2001 as part of a restoration project.

5.3.3. Field growth in the first season

Growth during the first season was, as expected, less than that for the second season for all plots (Fig. 5.8). One outlier in the 1999 plot (*Horsfieldia thorelii* - S236, not shown here), had much slower growth in second season than the first.

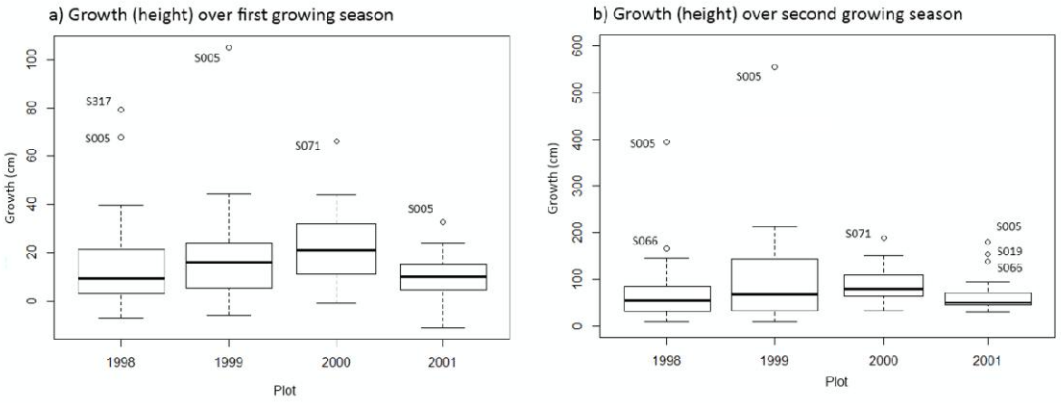


Figure 5.8: Growth rate in the field for 53 species planted in Doi Suthep-Pui National Park in 1998, 1999, 2000 and 2001 as part of a restoration project. Measurements were taken a) five and b) seventeen months after planting – after the first and second growing season respectively.

Growth in the first season after planting varied considerably, from negative growth (loss of height) to 69% of that in the second season. Growth over the first season was correlated with growth in the second season for the same plots in the 1998, 1999 and 2000 plots ($p<0.001$, $p<0.001$, $p=0001$ respectively), (Table 5.3).

To separate the effect of transplantation from that of environmental conditions in different years, growth for individual species in their first year after planting was compared with growth in the same year in their second year after planting. Thus; H12 for the 1999 plot was compared with H23 for the 1998 plot etc. Table 5.3). Results confirmed that species planted in 2001 had disproportionately low growth in the first year after planting compared to other plots (81% with less than 20% growth). However, results for the 1999 and 2000 plots differed from that when comparing growth rates in the same plot and indicated that those planted in 1999 had less inhibited growth (only 27% with less than 20% growth) and that 2001 had an intermediate level (52%).

Table 5.3: Relationships between growth in the first season and the second season after planting in the field for 53 species of tree from Doi Suthep-Pui National Park, raised in the nursery and planted as part of a restoration project in 1998, 1999, 2000 and 2001. (a) both within the same plot (but planted in different years) and in the same year (but planted in different plots). Significant correlations are marked in bold

Plot	(a) First season growth as a proportion of second season growth in the same plot			Percentage of species with less than 20% growth in the first season of that in the second season		Correlations between growth in the first and second season after planting for	
	Mean	Min.	Max	same plot	same year	same plot	same year
1998	0.175	-0.351	0.558	NA	57%	**0.655*** (<0.001)**	NA
1999	0.200	-0.442	0.695	27%	50%	**0.598*** (<0.001)**	**0.706** (0.008)**
2000	0.255	-0.017	0.563	52%	38%	**0.567** (0.001)**	**0.756*** (<0.001)**
2001	0.157	-0.158	0.398	81%	67%	0.297 (0.079)	0.371 (0.078)

Growth was considered for individual species planted in more than one year and indicated a wide range of behaviours between years, plots and species (Fig 5.8). When comparing 1999 & 2000 or 1999 & 1998, the plot with maximum growth for a species was mixed (Fig. 5.9 a &b). Growth in 1998 was faster than in 2000 or 2001 for most species (Fig, 5.9 c &f). Growth in 2001 was generally slower than that in other years (Fig. 5.9 d, e & f), except for a small number of slow-growing species (*Manglietia garrettii* - S007, *Ficus benjamina* - S029, *Ficus subulata* - S039 and *Castanopsis acuminatissima* - S270).

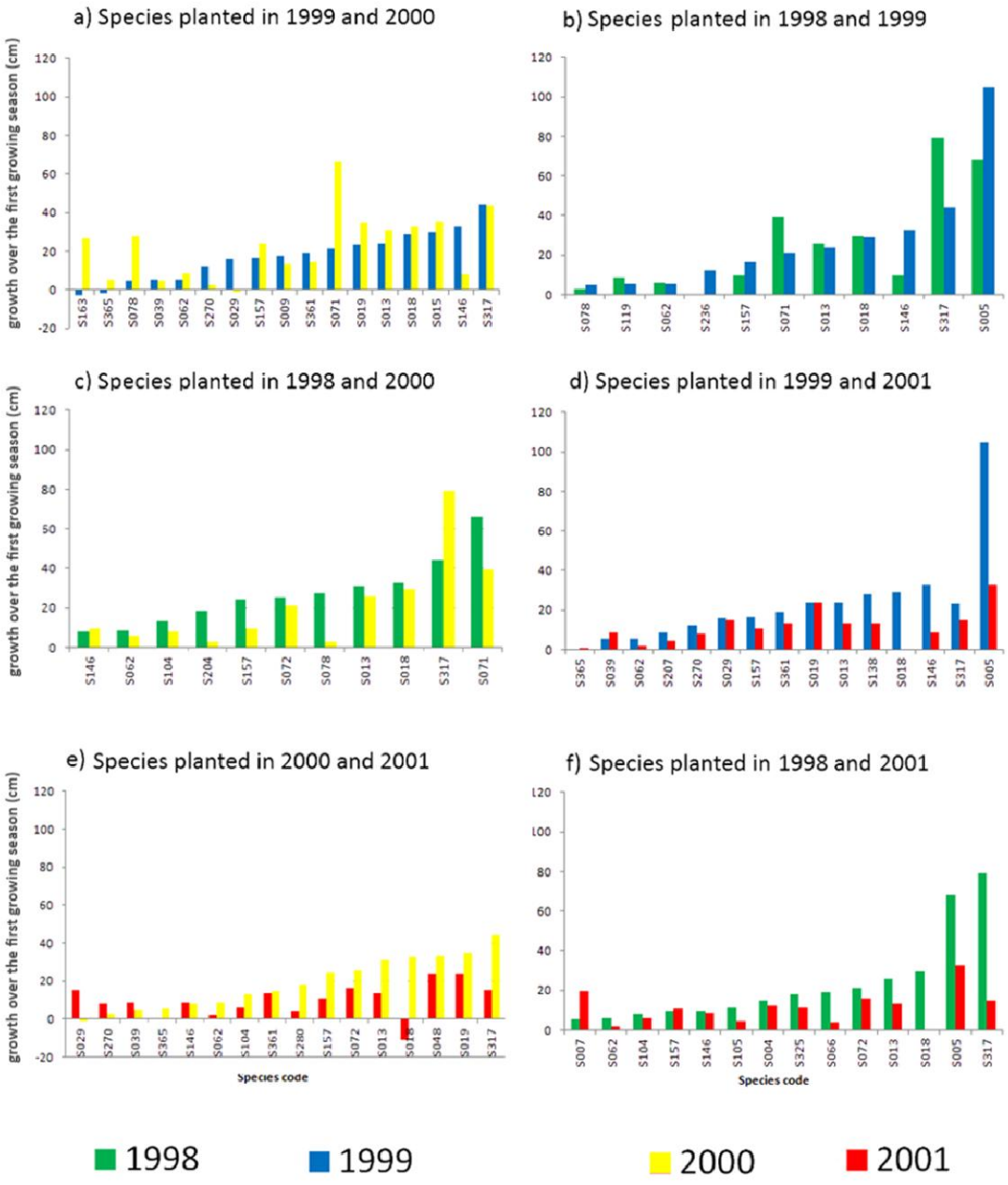


Figure 5.9: Comparisons of growth (height in cm) over the first season after planting in the field for species that were raised in the nursery and planted out in two different seasons as part of a restoration project in Doi Suthep-Pui National Park. The species that relate to the codes given are provided in table 5.1

5.3.4. Field growth in second season

Field growth during the second season after planting was, as expected, greater than that in the first season (Fig 5.8). Faster growing species grew more in the 1999 plot than in other plots. However, these few individuals did not affect the mean value sufficiently to create a higher mean growth rate in 1999 than other years. Instead, saplings had higher mean growth in the 2001 plot than other plots (Fig 5.8b).

When species planted in more than one year were plotted, growth was approximately 1.4 times faster in 1999 plots for species shared with the 1998 and 2001 plots (Fig 5.10 a & c). The relationship between growth rates in the 1999 and 2000 plots was more complex; the slope of the regression line was similar to those of between 1999 and the other two years but some taller species were not as fast growing in the 2000 plot and some slower growing species were not as slow growing as expected (Fig 5.10b). A similar pattern was observed between the 2000 plots and the 1998 and 2001 plots (not shown). Growth in the 1998 and 2000 plots were similar to each other (Fig. 5.10d).

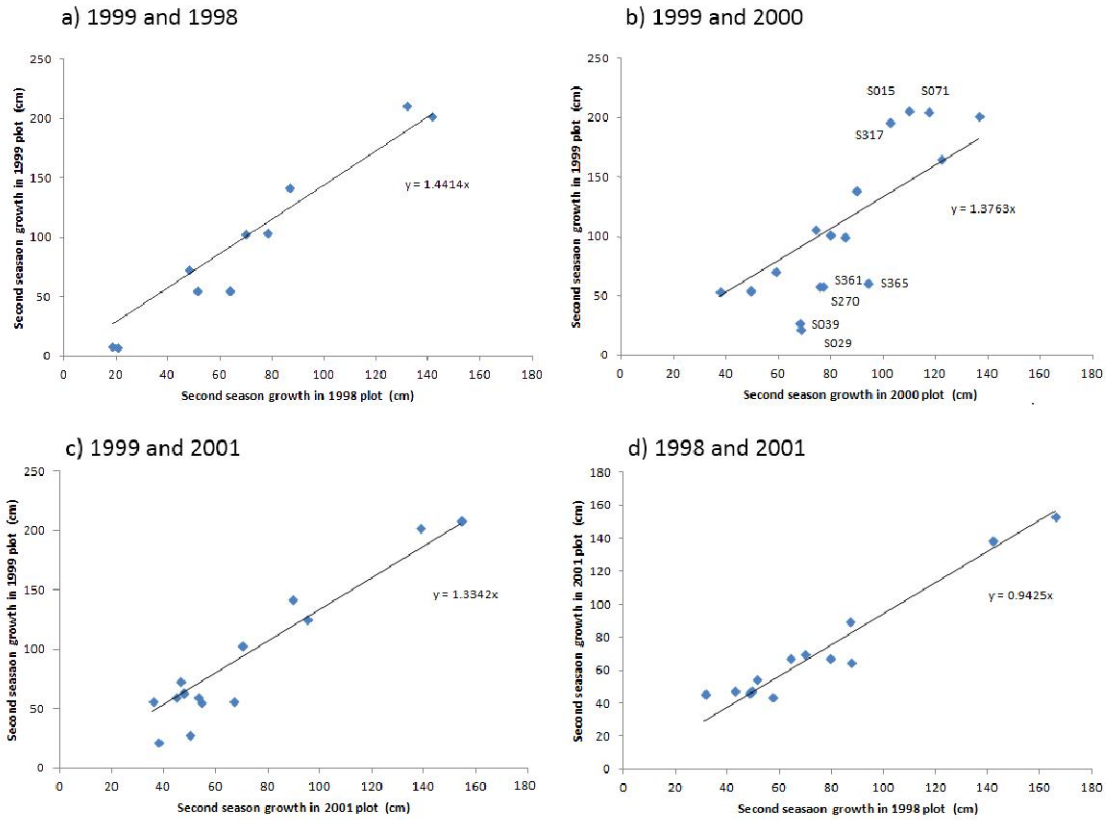


Figure 5.10: Regressions of growth (based on height) in the second season after planting out for species that were planted out in two different seasons

5.3.5. The 2000 plot

Due to the apparent difference in relationship between growth of faster or slower growing species in the 2000 and 1999 plots, these groups were considered separately. Of the 12 species with at least one instance of more than 125cm growth during the second season after planting, eight were planted in at least one of either 1998 or 1999 and at least one of either 2000 and 2001. Of these, all showed faster growth in 1998 and 1999. Species *Ficus semicordata* - S315, *Acrocarpus fraxinifolius* -S031, *Betula alnoides* - S048 and *Morus macroura* - S081 had fast growth in at least one year but were not included here as they were not planted in more than one year. These faster growing species all had faster growth in the 1999 and 1998 plots compared to the 2000 and 2001 plots (Table 5.4a).

Species with less than 35 cm growth over the second growing season were also considered. Of these 14 species (*Ficus benjamina* - S029, *Ficus subulata* - S039, *Aphanamixis polystachya* - S060, *Pterocarpus macrocarpus* - S092, *Helicia nilagirica* - S104, *Horsfieldia amygdalina* - S119, *Aglaia lawii* - S123, *Glochidion kerrii* - S179, *Markhamia stipulate* - S204, *Cinnamomum iners* - S218, *Horsfieldia* thorelii - S236, *Phoebe lanceolata* - S268, *Ficus heteropleura* - S372, *Phoebe cathia* - S379), only 4 were planted in either 1998 or 1999 and in either 2000 or 2001. All of these species were much slower growing in 1998 and 1999 than 2000 and 2001 (Table 5.4 b).

Table 5.4: Comparison of growth (height in cm) during the second season after planting for a) Fast growing species (species with more than 125cm growth in at least one plot) and b) slow growing species (species with less than 35cm growth in at least one plot) for 53 species of tree raised in the nursery and planted as part of a restoration project in Doi Suthep-Pui National Park. In a) the plot with most growth is marked in bold and in b) the plot with least growth is marked in bold. The species that relate to the codes given are provided in table 5.1

a) Fast growing species					b) Slow growing species				
	Year planted					Year planted			
Species	1998	1999	2000	2001	Species	1998	1999	2000	2001
S009	NA	**170.75**	121.86	NA	S029	NA	**22.64**	68.19	37.96
S015	NA	**212.2**	109.7	NA	S039	NA	**28.21**	67.78	49.8
S019	NA	**208.55**	136.39	154.38	S104	**31.11**	NA	48.86	45.31
S066	**165.85**	NA	NA	152.89	S204	**30**	NA	49.23	NA
S071	NA	**211.33**	117.34	NA					
S317	141.73	**202.83**	102.31	138.34					
S138	NA	**126.19**	95	NA					
S146	86.85	**143.06**	89.36	89.52					

5.3.6. Survival

Total survival rates for the 1999 plots was very low (37%), compared to other years (1998 = 68%, 2000 =56%, 2001 = 57%) due to the very high death rate in the first season after planting. In all other plots, most deaths occurred in the second year after planting. In the first year after planting, the range of seedling deaths was greater in the 2000 plot than in the 2001 plot. Survival over the second year was significantly greater in the 1998 plots than the 1999 and 2001 plots and the range of survival rates was significantly smaller in the 2001 plot compared to the 1998 and 2000 plots (Fig 5.11).

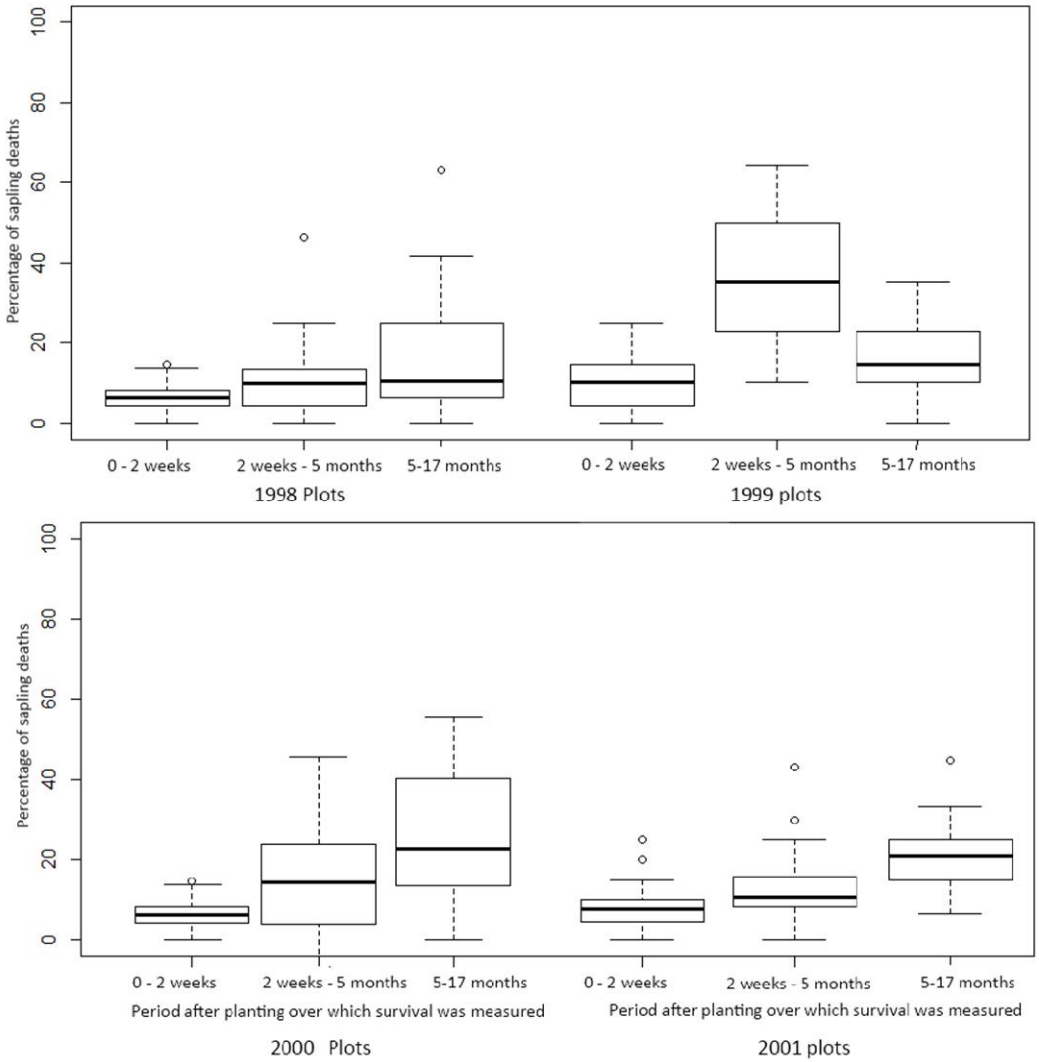


Figure 5.11: Percentage of sapling deaths occurring during the first two weeks after planting, first growing season after planting and second year after planting in saplings planted in 1998, 1999, 2000 and 2001 as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand as a percentage of the number of saplings planted.

5.3.7. Growth and survival over the first season after planting

For the 1999 plots, survival over the first growing season was correlated positively with survival over the first 2 weeks after planting ($p<0.001$). In the 2000 plot, there was a negative correlation ($p=0.028$). In the 1998 plot only, survival over the first growing season was positively correlated with growth over the same period ($p=0.019$), however, no relationships were identified between survival over the first growing season and growth rates either in the nursery or in the field in the second season after planting (Table 5.5). Comparisons of species planted in different years showed a positive correlation between first year survival in the 1998 and 2000 plots only ($p=0.011$).

Table 5.5: Correlations (Spearman) between survival of seedlings in each plot during the first season after planting and either survival of the first two weeks after planting or growth over the entire season for 53 species of tree from Doi Suthep-Pui National Park, raised in the nursery and planted as part of a restoration project in 1998, 1999, 2000 and 2001. Significant values are marked in bold

Plot	Correlation between survival of the first two weeks and the first growing season	Correlation between survival and growth over the first growing season
1998	0.162 (0.205)	**0.512** (0.003)**
1999	**0.577** (0.001)**	0.265 (0.078)
2000	-0.378* (0.028)	0.042 (0.419)
2001	-0.035 (0.436)	0.078 (0.359)

5.3.8. Growth and survival over the second season after planting

In both the 1998 and 1999 plots, there was a positive correlation between growth in the second year after planting and survival over the same period (1998 $p<0.001$, 1999 $p=0.004$). In the 2000 and 2001 plots, no such relationship occurred. In the 2000 and 2001 plots, there were no species with very slow grow or very fast growth. Also, there were no species with very low survival (Fig 5.11).

Comparisons of growth rates for fast and slow growing species were made (Table 5.4) which showed that the lack of very slow and very fast growing species in the 2000 and 2001 plots were due to differences in growth rates of particular species, not due to differences in species planted. Comparisons of survival rates for species with low survival were also made to investigate the lack of species with low survival in the 2000 and, in particular, the 2001 plot, where no species had lower than 60% survival.

Of the six species (*Aphanamixis polystachya* - S060, *Pterocarpus macrocarpus* - S092, *Horsfieldia amygdalina* - S119, *Garcinia mckeaniana* - S128, *Callicarpa arborea* - S156 and *Ficus heteropleura* - S372) with less than 50% survival over the second year in either the 1998 and 1999 plots, none were planted in 2000 or 2001. It was therefore impossible to assess whether these species would have had higher survival if planted in those years. However, the 2001 plot chart is suggestive of a potential relationship if species with lower survival had been planted (Fig 5.12).

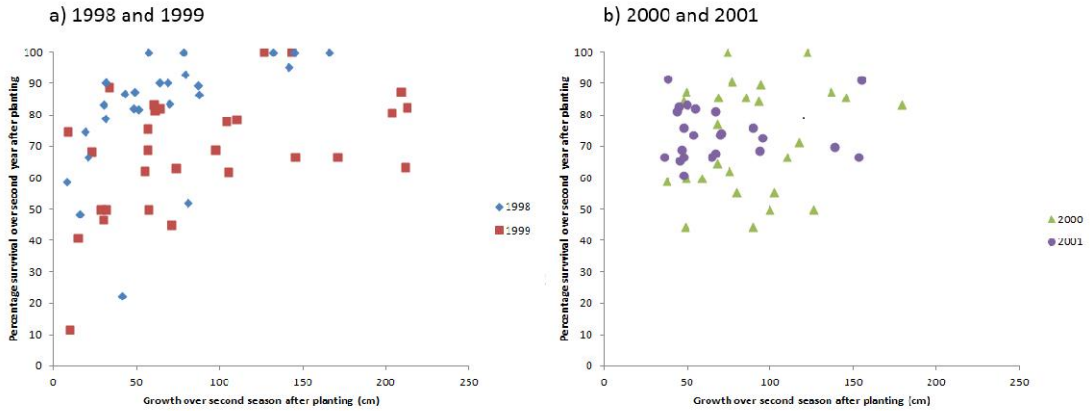


Figure 5.12: Relationship between survival and growth over the second growing season after planting in a) 1998 and 1999, and b) 2000 and 2001 for seedling planted as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand.

Of the seven species (*Sapindus rarak* - S013, *Ficus subulata* - S039, *Quercus semiserrata* - S062, *Gmelina arborea* - S078, *Heynea trijuga* - S157, *Cinnamomum caudatum* - S207and *Erythrina subumbrans* - S317) with between 50% and 60% survival in any plot, the plot with lowest survival varied, and no relationship could be seen between survival in one plot and survival in another (Table 5.6).

Table 5.6: Survival in the second season after planting for species that have had survival of between 50% and 60% on any year of planting for 53 species of tree from Doi Suthep-Pui National Park, planted as part of a restoration project in 1998, 1999, 2000 and 2001.

Species	1998	1999	2000	2001
S013	82%	63%	**60%**	69%
S039	NA	**50%**	64%	83%
S062	82%	**59%**	69%	82%
S078	**NA**	100%	62%	**55%**
S157	90%	75%	**60%**	81%
S207	NA	**50%**	NA	67%
S317	95%	80%	**56%**	70%

5.3.9. Nursery growth and performance in the field

Nursery growth rate was correlated with growth in the second year after planting for all plots except the 2000 plot, but over the first season for the 1999 plot only. Survival in the first year after planting was negatively correlated with nursery growth rate in the 2001 plot only, and positively correlated with survival over the second year after planting in the 1999 plot only. The loss of growth during the second season after planting (H12/H23) was negatively correlated with nursery growth in both the 1999 and 2001 plots (Table 5.7). Height at planting was uncorrelated with performance.

Table 5.7: Spearman rank correlations between growth in the nursery and both survival and growth in the field for species planted in Doi Suthep–Pui National Park in 1998, 1999, 2000 and 2001. NGRH = Nursery growth rate (height), H23= Growth (height) second growing season, S12 = Survival over the first growing season and S23 = survival over the second growing season. Significant correlations are marked in bold

Measures	Year Planted 1998 Correlation (P)	n	1999 Correlation (P)	n	2000 Correlation (P)	n	2001 Correlation (P)	N
H12	0.336 (0.054)	27	**0.431** (0.010)**	29	0.263 (0.108)	25	-0.173 (0.209)	28
H23	**0.440* (0.017)**	27	**0.758*** (<0.001)**	29	0.092 (0.332)	**25**	**0.342* (0.037)**	28
H13	**0.470* (0.012)**	27	**0.740*** (<0.001)**	29	0.116 (0.295)	**25**	**0.363* (0.040)**	28
S12	-0.030 (0.443)	27	0.097 (0.308)	29	0.155 (0.229)	**25**	**-0.407* (0.015)**	28
S23	0.301 (0.076)	27	**0.489** (0.003)**	29	-0.175 (0.201)	25	-0.170 (0.193)	28
H12/H23	0.123 (0.289)	27	**-0.333* (0.039)**	29	0.258 (0.122)	**25**	**-0.481** (0.009)**	28

5.4. Discussion

The survival and growth of 53 species of tree planted as part of a restoration project in 1998, 1999, 2000 and 2001 were investigated at different stages of the restoration process. Individual species planted in more than one year were considered to assess the influence of plot differences against species differences. Rainfall at the beginning of the growing season, (May) was average in 2001 and 1998 and exceptionally high in 1999. From July onwards, rainfall dropped to below average in 1998 and 1999 but was high in 2001. Rainfall in 2002 was high in both the early and late wet season. The influence of rainfall on performance has been investigated, reasons for these relationships have been suggested and the validity of models which predict tradeoffs or correlations between growth and survival in response to differing environmental limitations has been assessed.

5.4.1. Performance in the Nursery

The similarities in mean and range of growth rates in the nursery between planting years suggest that a similar mix of species were planted in each year and that watering regimes and pathogen control measures were equally effective in each year. As the Framework Species Approach suggests that seedlings should be planted when they are between 30 and 60 cm tall (Goosem & Tucker 1995), the slight difference in height at planting between years is probably due to improved fine-tuning of propagation schedules to ensure appropriately sized seedlings in late June. The two very fast growing species in the nursery, *Hovenia dulcis (S018) and Prunus cerasoides (S071)* both have orthodox seeds and display epigeal germination, both traits classically associated with pioneer species and the potential for fast growth (Swaine & Whitmore 1988; Bazzaz 1991; Whitmore 1998). Whilst S071 maintained very fast growth in the field, S018 slowed considerably in the second season after planting. Consideration of other factors such as seed characteristics, specific leaf area and wood density, which have all been linked to growth rate, may be valuable in accounting for their unusually fast growth in the nursery and contrasting later performance (Enquist *et al.* 1999; Westoby *et al.* 2002; Wright *et al.* 2004).

For nursery–raised seedlings, soil conditions and watering regimes were designed to encourage maximum growth and herbivores are discouraged through a variety of methods (Elliott *et al.* 2002). Nursery growth rates approximate to the fastest potential growth rate in early life and may therefore be more valuable than observed field growth in identifying species strategies. However, early growth may be aided by presence of extensive within-seed resources and differences between epigeal and hypogeal species may be observed (see Chapter 3). Some species with large seeds show an early fast growth (Foster & Janson 1985; Westoby, Leishman & Lord 1996; Kisdi & Geritz 2003) which slows down in relation to other species as seed resources reduce and other species respond better to light availability (Kitajima 1994; Paz & Martinez-Ramos 2003; Baraloto, Forget & Goldberg 2005; Poorter & Rose 2005). Therefore, care must be taken to consider these factors when relating nursery to later performance. Here, the relationship between nursery performance and later growth was variable, it was useful in predicting field growth in the 1998 and 1999 plots only and survival in the 1999 plot only.

By considering other factors known to affect early growth rates such as seed maternal investment (Foster & Janson 1985; Westoby, Leishman & Lord 1996; Kisdi & Geritz 2003), it may be possible to produce a more accurate prediction of potential field growth rate in optimal conditions. An understanding of the environmental factors that affect actual growth rates should allow the creation of a model that predicts field growth in all years.

5.4.2. Survival in the first growing season of the 1999 plot

Survival in the first season was very low in the 1999 plots and comparisons of individual species confirmed that this was due to actual species performance rather than the planting of different species. In the 1999 plot only, survival of the first two weeks after planting and the rest of the growing season were correlated. Furthermore the deaths in the 1999 plot were not mirrored in the second season performance of the 1998 plot. These results point to the cause of sapling death in 1999 being related to initial problems with establishment. As growth rates in the 1999 plot were reasonably high, it is suggested that this cause of sapling loss was

brief and did not affect later growth in the field. This period of low survival was not correlated with any measures of growth, and therefore, does not support any of the suggested models (Swaine & Whitmore 1988; Kobe *et al.* 1995).

The most noticeable characteristic of the weather in 1999 was the very high rainfall in May of that year. It is suggested that this may have affected survival but the mechanism through which it did this is unclear. An unusually wet early rainy season (whilst seedlings were still in the nursery) may have affected the performance of seedlings after transplant in a number of ways including; (a) increased levels of pathogens (Swinfield *et al.* 2012), (b) decreased effectiveness of hardening off (Anderson & Helms 1994) and (c) water-logging. In order to acclimatise seedlings to field conditions, they were given less water in the weeks leading to transplantation (Elliott *et al.* 2003). However, as the seedlings in the nursery were not under cover, seedlings would have received a great deal of water as rainfall during this period. This could have both confounded attempts to harden-off seedlings and exposed them to water-logging. Investigation of species traits linked to poor survival in the 1999 plots known to affect transplantation success, such as root traits or pathogen resistance, may aid in understanding the mechanism for this effect.

5.4.3. Growth in the first year after planting

Growth over the first growing season is predicted to be less than that in the second season due to both the shorter period over which growth was measured and the smaller size of seedlings at the beginning of the first season (Westoby, Leishman & Lord 1996; Leishman *et al.* 2000). However, the high variability of the ratio of first to second years growth between species suggests that some transplant shock occurred and that this varied between both species and plots. Transplant shock or stress is a suite of negative responses to seedling transplantation that include reduced growth, leaf shedding and increased mortality (Rietveld 1989). The level of transplant shock reduced-growth appeared greatest in the 2001 plot, a year of high rainfall, despite the predicted correlation between transplant shock and drought-induced stress (Burdett, Simpson & Thompson 1983; Grossnickle 1988).

5.4.4. Growth in the second season after planting

Growth rates in the 1999 plot were greater than the 2001 and 1998 plot in a consistent fashion (growth was approximately 1.4 time faster) in all species. As the rains came early in the 2000 season (over which the growth of the 1999 plot occurred) and finished late, it is likely that this caused a longer growing season as has been found in other seasonally dry forests (Maass *et al.* 1995). However, the 2000 plot had a more variable relationship with growth in other years, which was confirmed as being linked to performance rather than to species selection. As the 2000 plot experienced its majority of growth during 2001, this points to a link with the observed low growth rate over the first growing season in the 2001 plots. There is ample evidence, therefore, that 2001 was an unusual year, but the question still remains why.

The 2001 growing season was very wet. However, the similarly wet 2002 did not appear to affect performance in a similar way. Consideration of plant traits linked to performance in 2001 may help to explain this discrepancy. Fungal pathogens, annual weeds and insects have been shown to increase with rainfall (Givnish 1999; Swinfield *et al.* 2012) which may have reduced performance in 2001 for fast growing species, whilst the increased rainfall assisted shade tolerant species. Investigation of key traits linked to pathogen resistance may be helpful in explaining the difference in performance in the 2000 plot.

5.4.5. Growth and survival correlations

Growth and survival over both years were closely positively correlated in the 1998 and 1999 plots, where both growing seasons had low rainfall; in dry years, fast growing species also had high survival. If slow growth is taken as an indication of shade tolerators (Niinemets & Valladares 2006) and fast growth an indication of pioneer species (Swaine & Whitmore 1988), this conflicted with the trade-off between robust and fast growth suggested by the CSR model (Grime 1977) and growth-survival hypothesis (Kobe *et al.* 1995), and supports the prediction that there will be a trade-off between traits associated with drought and traits associated with shade tolerance (Smith & Huston 1989; Abrams 1994; Abrams &

Kubiske 1994; Kubiske, Abrams & Mostoller 1996; Niinemets, Kull & Tenhunen 1998). The correlation occurred only in the second season after planting which supported a link to potential rather than actual growth predicted by the models.

The lack of correlation between growth and survival in years with high rainfall (2000 and 2001 plots, 2001 and 2002 growing seasons) appears due to a combination of differences in species planted and differences in performance. Whilst in the 2000 plot there was no evidence for a correlation between growth rate and survival, the 2001 plot result suggest that, if lower surviving species had been planted, a correlation may have been observed.

5.4.6. Conclusions

Survival and growth were positively correlated in some years and plots and negatively correlated in others. Therefore, no blanket negative correlation was found that supported the growth/survival trade-off. Similarly, the categories defined within the CSR triangle are not supported by the findings.

Growth rates and survival appear to be linked, both in the nursery and in the field in ways predicted by their adaptations for the specific environmental limitations of drought and shade. Differences in behaviour between plots appear to support these hypotheses, but further work is needed to confirm the relationship between specific plant traits, growth and survival.

The role of fungal pathogens and insects as an important cause of seedling death is suggested as a possible area of further research in conjunction with drought and shade tolerance characteristics.

6. Seed and germination characteristics predicting growth and performance in a seasonally-dry tropical forest restoration scheme

6.1. Introduction

6.1.1. Seed characteristics

The Framework Species Approach (FSA) to forest restoration involves the planting of a mixture of nursery-raised seedlings to provide both fast-growing trees (that provide shade) and early-fruiting trees with fleshy fruit (to attract frugivores and bring in new plant species through animal-mediated facilitation), (Goosem & Tucker 1995). Whilst seed germination, and seedling establishment are critical stages in the life of a plant during natural seeding (Silvertown *et al.* 1993), the use of nursery-raised seedlings for forest restoration removes this stage of development as a limiting factor. However, seed, germination and early establishment characteristics are still important considerations because;

(a) Seedlings still have to be raised in the nursery. For this to be efficient, the selected species must have fast germination, high germination success, fast early-growth and good survival. The nursery techniques used should aim to maximise performance for the species raised.
(b) Seedlings should perform well after planting in the field. Seed traits may be good indicators of traits such as growth rate, survival, early fruiting and copious fruiting.

Here, fruit, seed and germination traits were investigated as a predictor both of germination and growth rates in the nursery and as an indicator of performance in the field for a restoration scheme in the seasonally-dry tropical forests of northern Thailand. Predicted links between seed and germination traits were assessed for their applicability to seasonally-dry tropical forests of northern Thailand, and links between fruiting phenology and seed traits were explored.

6.1.2. Germination and seed size

Larger seeds have a higher maternal investment per seed and have been linked to higher germination rates (Westoby *et al.* 2002). Larger seeds also tend to exhibit hypogeal germination where cotyledons provide metabolic reserves for growth, whereas smaller seeds tend to have epigeal germination where foliar cotyledons act as photosynthetic organs (Ibarra-Manriquez, Ramos & Oyama 2001; Zanne, Chapman & Kitajima 2005). The smaller-seeded and epigeal species may initially grow slower due to their reduced metabolic reserves (Foster & Janson 1985; Westoby, Leishman & Lord 1996; Kisdi & Geritz 2003), but may overtake quickly due to their ability to respond more quickly to light availability (Kitajima 1994; Paz & Martinez-Ramos 2003; Baraloto, Forget & Goldberg 2005; Poorter & Rose 2005).

Larger seeds have also been linked to better early survival than smaller seeds (Oni & Bada 1992; Milberg & Lamont 1997; Westoby *et al.* 2002) due to having greater tolerance for defoliation (Armstrong & Westoby 1993), and a number of mechanisms to explain this have been proposed. The 'reserve effect' hypothesis, suggests that larger seeds maintain carbohydrates and nutrients that allow for better recovery from damage (Westoby, Leishman & Lord 1996; Green & Juniper 2004) . The 'metabolic effect' hypothesis, suggests that larger seeds occur in species with a lower metabolic rate and that this allows seedlings to maintain their carbon balance. The seedling size effect (Westoby, Leishman & Lord 1996; Leishman *et al.* 2000), suggests that larger seeds occurs because larger seeds produce larger seedlings that are less vulnerable to damage. Phylogenetic studies suggest that seed size along with other reproductive traits is a conserved characteristic, and that this may limit adaptation (Lord, Westoby & Leishman 1995; Moles *et al.* 2005; Ackerly 2009).

6.1.3. Period of germination

It is predicted that large-seeded species will be more vulnerable to predation than smaller seeds (Louda 1989; Blate, Peart & Leighton 1998) and that they therefore tend towards faster germination. Conversely, small-seeded species, which are less vulnerable to predation, will have a longer dormancy period (Venable & Brown 1988; Rees 1994). Seeds may have evolved thick seed coats as a defence from insect predation and phenolic compounds in the seed coat may contribute to inhibition of micro-organism growth (Mohamed-Yasseen *et al.* 1994).

Variation in germination period is considerable between species (Vazquez-Yanes & Orozco-Segovia 1993) suggesting a variety of strategies associated with trade-offs between these threats. Asynchronous germination spreads the risk between the two conflicting risks (Cohen 1966; Clauss & Venable 2000; Venable 2007). Consequently, it might be expected that this competitive trait has co-evolved with other plant traits that are involved directly in regeneration success such as high seed mass. Germination rates may be greater in the shade than the sun, which has been linked to the higher risk of desiccation in full sunlight (Augspurger & Kelly 1984). However, some species remain within the soil seedbank until dormancy is broken by sunlight. This "photoblastic response" is linked to pioneer species which colonise land immediately after disturbance (Swaine & Whitmore 1988), yet a broader interpretation of pioneer species concept does not usually require a photoblastic response (Brokaw 1987; Daws *et al.* 2002; Pearson *et al.* 2003). However, an alternative theory for higher germination in exposed conditions is that wetter and shadier conditions have been linked to a higher risk of "damping off", a fungal condition that kills seeds before or shortly after germination (Taher & Cooke 1975), as well as an increase in other pests. Alternatively, germination rates may be higher in the shade. This has been linked to a number of cues including less extreme temperature drops at night and better soil moisture retention (Kos & Poschlod 2007).

6.1.4. Field performance

As restoration sites are usually open ground or areas containing only weeds, pioneer species (species that colonise areas immediately after disturbance) should perform well. The original definition of pioneer species was based only on germination and seedling characteristics (Swaine & Whitmore 1988); other authors added more characteristics, such as leaf types and growth rates, to the classification. Pioneer species generally have small seeds, fast growth and various adaptations for growth in open conditions (Bazzaz 1991; Whitmore 1998) such as drought tolerance (Leishman & Westoby 1994a). Larger seeds have also been linked to climax species and better survival in shade (Leishman & Westoby 1994b). It has also been predicted that seeds of pioneer species will be orthodox with epigeal germination and persist in the seed-bank (Swaine & Whitmore 1988).

In seasonally-dry tropical forest, recalcitrant seeds are more likely to be shed during the rainy season and orthodox species during the dry season (Ray & Brown 1995). It has been suggested that germination will be timed primarily during the rainy season to ensure maximum survival (Garwood 1983). Garwood, (1983) further suggested that pioneer species tended to germinate early in the wet season whereas under-storey species germinated over the entire season, as did animal-dispersed species.

6.1.5. Hypotheses and aims

The aim here is to assess whether;

- Seed characteristics may predict germination performance
- Seed characteristics and germination performance may predict nursery performance
- Seed characteristics, germination performance and nursery performance may predict field performance

The following hypotheses were tested;

Species with better germination in the light are “pioneers” and possess other pioneer characteristics such as;

- Faster growth
- Better survival in dry years
- Worse survival in wetter years
- Thin seed coats

Predictions of germination behaviour

- Recalcitrant species germinate better in full shade
- Range will be larger for smaller seeds
- MLD will be shorter for larger seeds
- MLD will be correlated with seed coat thickness

Predictions of growth

- Recalcitrant species will have slower growth than orthodox species
- Species with hypogeal germination will have faster growth in the nursery than those with epigeal growth but the opposite will be true in the field.
- Growth rates in the nursery will correlate with seed size

Predictions of survival

- Seed size is correlated with survival in the first year after planting
- Recalcitrant species have better survival in wet years

Predictions of phenology

- Wind distributed seeds will be shed in April
- Recalcitrant seeds are more likely to be shed during the rainy season and orthodox species during the dry season
- MLD and time of fruiting will lead to species germinating in the wet season
- Pioneer species germinate early in the wet season whereas under-storey species germinated over the entire wet season

6.2. Methods

6.2.1. Doi Suthep-Pui National Park

The Doi Suthep-Pui National Park (created in 1981) is an area of approximately 260 km^2 of seasonally-dry tropical forest near Chiang Mai in northern Thailand (18.83203°N / 98.88805°E) and ranges from 340 to 1680m a.s.l (Maxwell & Elliott 2001). Whilst annual rainfall is high, rainfall in January and February can be as low as 6 mm a month, rising after the start of the monsoon in April or May to a peak of 275mm in August before dropping swiftly from October. The dry season is sub-divided into the cool-dry season (November–January) where maximum temperatures range from 30 ^{o}C to 32 ^{o}C and the hot-dry season (February– April), with a maximum daily temperature of between 30^{o}C and 39^{o}C (Fig. 6.1.).

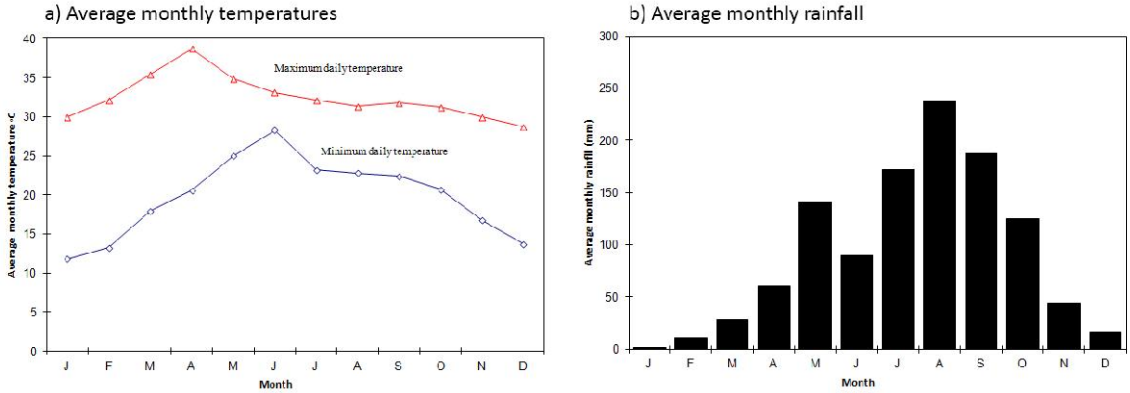


Figure 6.1: Monthly (a) maximum and minimum daily temperature and (b) rainfall in the Chiang Mai area of northern Thailand. Based on records from between 1952 and 1997– (Maxwell & Elliott 2001)

This study covers species planted from 1998 to 2001. Rainfall patterns varied significantly between years. In 1998, the peak in rainfall in May was as expected but rainfall later in the wet season was slightly lower than average. In 1999, after a very rainy May, the period from June to September experienced lower rainfall than usual. In 2000 a high early peak led to a large drop in July and a reduced and delayed later rainy season. The late rainy season in 2001 was particularly wet and there was not a large drop in rainfall between the first and second peak. Both the early and late peaks of rainfall were high in 2002 (Information Services - Thai Meteorological Office-personal communication 2013).

6.2.2. Germination and performance data

Germination performance data were extracted from the FORRU database (FORRU, 2011); the result of trials on over 400 species between 1996 and 2001 where germination in full shade was compared with that under partial shade. For the partial shade treatment, seed trays were placed on top of concrete benches, under a transparent plastic roof, whilst for the deep shade treatment, trays were placed underneath the same benches, which were screened around the sides with black plastic shade netting. For each of the two shade treatments, 72 seeds were divided into three replicate batches of 24, which were randomly assigned to different benches and watered daily (Blakesley *et al.* 2000). Seeds were observed on a daily basis and germination recorded when seedlings broke the soil surface. From these germination records, a number of key measurements were extracted (Table 6.2) to reflect the differing germination rates, dormancy periods and synchronicity of germination when in full shade or semi-shade conditions. A final measurement Shade:Sun GR, where Shade is germination under full shade and Sun is germination under partial shade, reflects the preferred germination conditions for a species.

Selected species from these trials were grown on in the nursery to planting-out height of approximately 30-60 cm tall. Here, growth rate in the nursery was estimated from mean germination time, time in the nursery and height measured two weeks after planting in the field. The species described here were planted in the field from 1998 to 2001. Approximately 30 species were planted in each year, with some variations in species selection between years (Table. 6.1). Saplings were monitored for survival and height two weeks after planting in order to assess transplantation survival and provide initial field height measurements. Monitoring was repeated in November of the planting year (+ five months after planting) to assess survival and growth after a single growing season and a final measurement was made in November of the year after planting (+ 17 months after planting) to assess the survival and growth after two growing seasons (see chapter 5 for details).

The 54 species for which data have been collected (Table 6.1) covered 23 families, with many families containing only a single representative. Species were placed in four broader clades (Rosids, 35 species,; Asterids, 7 species; Eudicots, 1 species and Magnoliids 10 species using the Angiosperm phylogeny Group System 111 (Bremer *et al.* 2009)

Table 6.1: Species of seedling planted in 1998, 1999, 2000 and 2001 as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand. Species code provided in brackets.

	Planted in each year					Planted in each year			
Species	**98**	***99***	**00**	**01**	***Species***	**98**	***99***	**00**	**01**
Bischofia javanica (S004)	ü			ü	*Garcinia mckeaniana (S128)*	ü			
Melia toosendan (S005)	ü	ü		ü	*Michelia baillonii (S138)*		ü		ü
Manglietia garrettii (S007)	ü			ü	*Nyssa javanica (S146)*	ü	ü	ü	ü
Macaranga denticulata (S009)		ü	ü		*Callicarpa arborea (S156)*		ü		
Diospyros glandulosa (S012)	ü				*Heynea trijuga (S157)*	ü	ü	ü	ü
Sapindus rarak (S013)	ü	ü	ü	ü	*Machilus bombycina (S163)*		ü	ü	
Balakata baccata (S015)		ü	ü		*Glochidion kerrii (S179)*		ü		
Hovenia dulcis (S018)	ü	ü	ü	ü	*Markhamia stipulata (S204)*	ü		ü	
Rhus rhetsoides (S019)		ü	ü	ü	*Cinnamomum caudatum (S207)*		ü		ü
Ficus benjamina (S029)		ü	ü	ü	*Cinnamomum iners (S218)*	ü			
Acrocarpus fraxinifolius (S031)		ü			*Horsfieldia thorelii (S236)*	ü	ü		
Ficus subulata (S039)		ü	ü	ü	*Phoebe lanceolata (S268)*	ü			
Betula alnoides (S048)			ü	ü	*Castanopsis tribuloides (S269)*			ü	
Aphanamixis polystachya (S060)	ü				*Castanopsis acuminatissima (S270)*		ü	ü	ü
Quercus semiserrata (S062)	ü	ü	ü	ü	*Lithocarpus elegans (S280)*			ü	ü
Spondias axillaris (S066)	ü			ü	*Ficus semicordata (S315)*			ü	
Prunus cerasoides (S071)	ü	ü	ü		*Erythrina subumbrans (S317)*	ü	ü	ü	ü
Ficus altissima (S072)	ü		ü	ü	*Eugenia albiflora (S325)*	ü			ü
Gmelina arborea (S078)	ü	ü	ü		*Castanopsis calathiformis (S335)*	ü			
Morus macroura (S081)			ü		*Lithocarpus fenestratus (S337)*		ü		
Eurya acuminata (S086)	ü				*Ficus glaberrima (S361)*		ü	ü	ü
Pterocarpus macrocarpus (S092)		ü			*Ficus racemosa (S365)*		ü	ü	ü
Alseodaphne andersonii (S101)	ü				*Ficus superba (S368)*			ü	
Helicia nilagirica (S104)	ü		ü	ü	*Ficus abellii (S370)*			ü	
Sarcosperma arboreum (S105)	ü			ü	*Ficus heteropleura (S372)*		ü		
Horsfieldia amygdalina (S119)	ü	ü			*Phoebe cathia (S379)*		ü		
Aglaia lawii (S123)	ü				*Ficus hispida (S380)*		ü		

6.2.3. Seed size and weight measurements

Seed trait data from the FORRU database (FORRU, 2011), and the Royal Botanic Gardens Kew Seed Information Database (Royal Botanic Gardens Kew 2008), were augmented with seeds collected in the field and from herbarium specimens. Where seed samples were herbarium specimens, degradation reduced the validity of seed dry weight as an appropriate measure of seed size. Seed volume, was therefore used as an alternative measure. To obtain seed coat measurements, seeds were broken and seed coats were measured under a microscope (due to the variability of seed coat thickness, this was at a variety of appropriate magnifications). Seed functional thickness included protective layers that, whilst not technically a seed coat performed the same function of protecting the seed after dispersal (e.g. the dry fruit of nuts and the stone of drupes) (Table 6.2).

6.2.4. Categorical data

Categorical data were extracted from a variety of sources including the Royal Botanic Gardens Kew Seed Information Database (Royal Botanic Gardens Kew 2008), FORRU database (FORRU, 2011), Flora of China (Zhengyi, Raven & Deyuan 1994+) and Flora of Thailand (Flora of Thailand Editorial Board 1970+). Data were augmented using field and herbarium samples. At least two sources were required for each species to confirm membership of a category.

Germination behaviour here refers to hypogeal or epigeal germination. Whilst some species exhibited intermediate or unusual germination behaviour, for the purposes of this study, only these two categories were used, with an emphasis on the photosynthetic capability of the cotyledons being used to classify species in cases of interim characteristics. Seed storage behaviour was categorised as either orthodox or recalcitrant. Species identified as able to survive desiccation but with a limited tolerance for very low temperature were included in the orthodox species category. Species were categorised as having either “dry”, “thinly fleshy” or “fleshy” fruit. Again, a functional approach has been taken and species with fleshy arils or other auxiliary structures were classified as “thinly fleshy” (Table 6.2).

Table 6.2: Seed and fruit traits and measures of growth and survival for 54 species of tree found in Doi Suthep-Pui National Park that were included in germination and growth trials by the Forest Restoration Research Unit (FORRU).

Measurement	Units	Calculation
Fruit fleshiness	Categorical	Fleshy, thinly fleshy, dry
Seed dispersal mechanism	Categorical	Animal, Non-animal, Mixed
Diaspore type	Categorical	Seed, Fruit, Seed with Aril
Seeds in diaspore	Count	Mean seed disapore number
Seed storage behaviour	Categorical	Orthodox, Recalcitrant
Seed dry mass	g	Direct measurement
Seed external volume	mm^2	4/3 π *length* width*depth
Seed coat thickness	µm	Thickness of seed coat only
Seed internal volume	mm^2	As for seed external volume but with each dimension minus seed coat thickness*2.
Functional seed coat thickness	µm	Thickness of seed coat and other protective covering of the diaspore. E.g. a stone.
Germination type	Categorical	Epigeal, Hypogeal
Germination rate in partial shade (Sun GR)	Percentage	Percentage of seeds to successfully germinate
Germination rate in full shade (Shade GR)	Percentage	Percentage of seeds to successfully germinate
Median length of dormancy in partial shade(Sun MLD)	days	Number of days from seed planting to the germination of the median seed
Median Length of dormancy in full shade (Shade MLD)	days	Number of days from seed planting to the germination of the median seed
Germination range in partial shade (Sun range)	Days	Days from germination of the first seed to when 75% of eventual germination was completed.
Germination range in full shade (Shade range)	Days	Days from germination of the first seed to when 75% of eventual germination was completed
Shade GR:Sun GR	Ratio	Shade germination rate/sun germination rate
Nursery growth rate (NGRH)	cm/days	Height1/Nursery growing time
Age at first flowering	years	Extracted from the FORRU database
Clade	Categories	Assigned using APG 111 system
Mean fruiting month	Categories	Month with highest level of ripe fruit
Survival in first year (S12)	Percentage	Survival at 5 months -Survival at 2 weeks*100
Survival in the second year (S23)	Percentage	Survival at 17 months-Survival at 5 months*100
Growth - first year in field (H12)	cm	Height after first year - Height after 2 weeks
Growth - second year in field (H23)	cm	Height after second year - Height after first year
Seasonal growth difference	cm	Growth in first season /growth in second season

6.2.5. Statistical analysis

Correlations between continuous traits were performed using the Spearman rank correlation method due to heavy skewing and the existence of outliers in most traits.

Where assessments were made of whether three or more samples differed significantly, the non-parametric method (Kruskal-Wallis one-way analysis method) was used, because of the highly-skewed nature of most of the continuous trait data used. Where two samples were compared, the Mann-Whitney U-test was used.

Binomial logistic regression, a form of generalised linear modelling (function 'glm', family binomial) within the R statistical environment (R Development Core Team, 2012) was used to derive relationships between continuous and categorical traits and specifically, to identify redundancy in explanatory traits through the comparison of AIC values using ANOVA (test =χ^2) to ascertain whether the model with both explanatory traits was more accurate in its predictions. All traits were normalized to a scale of 0.1 to 1.1 before analysis to account for the very large scale differences. The parsimony protocol outlined by Crawley (2007) was used to simplify the model, i.e. by removing any redundant variables and producing the Minimum Adequate Model (MAM).

6.3. Results

Seed dry weight is a commonly used functional trait. Here seed volume is presented as an alternative measure where seed weight is unavailable. The correlation between the two traits was very highly significant ($p<0.001$) and no differences in results were found when seed volume was used in the place of seed dry weight for the 30 species for which both measures were available. Seed volume has therefore been used here as it allowed for more species to be included in the analysis.

6.3.1. Seed characteristic relationships

Here, almost all orthodox species had epigeal germination and almost all recalcitrant species had hypogeal germination ($p<0.001$), (Fig. 6.2). Only a single species was both hypogeal and orthodox; (*Erythrina subumbrans* - S317) and only three were both epigeal and recalcitrant; (*Spondias axillaris* - S066, *Sarcosperma arboretum* - S105 and *Michelia baillonii* - S138). Due to the consistent relationship between germination type and seed storage behaviour, relationships of other seed traits to these two characteristics are also consistent. From this point on, only results relating to seed storage behaviour will be discussed. It should be assumed unless otherwise stated that the relationships described also occur with germination type.

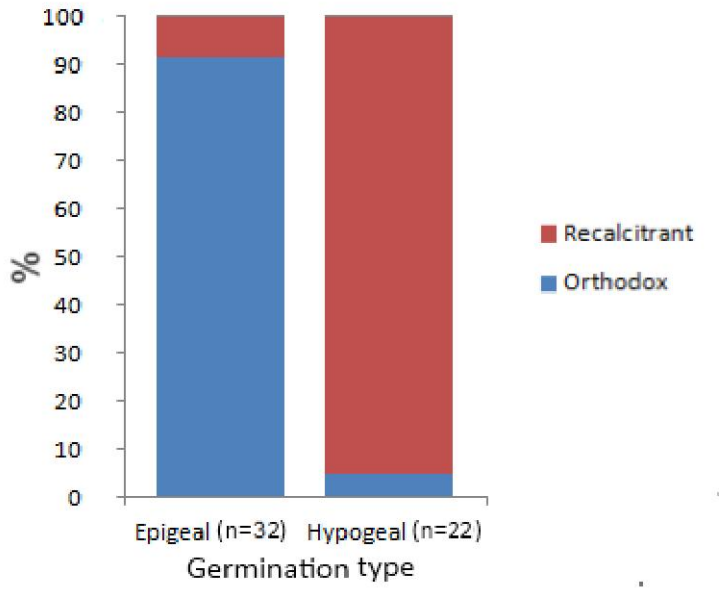


Figure 6.2: Co-occurrences of seed related characteristics for 54 species of tree found in Doi Suthep-Pui National Park.

Seed size, (total volume and internal volume) were significantly larger in species with orthodox seeds than recalcitrant seeds ($p<0.001$ in both cases),(Table 6.3 and Fig. 6.3a). Seed size also differed significantly with clade with Asterids and Rosids having smaller seeds and Magnoliids having larger seeds (Fig. 6.3b). Clade was also strongly linked to seed storage behaviour; all but one Asterid, and all but one Magnoliid were orthodox. Rosids were more mixed, with 22 of 36 being recalcitrant and the other 14 being orthodox. Use of a bionomial logistic regression showed that the addition of clade added significantly to the model predicting seed storage behaviour ($p< 0.05$).

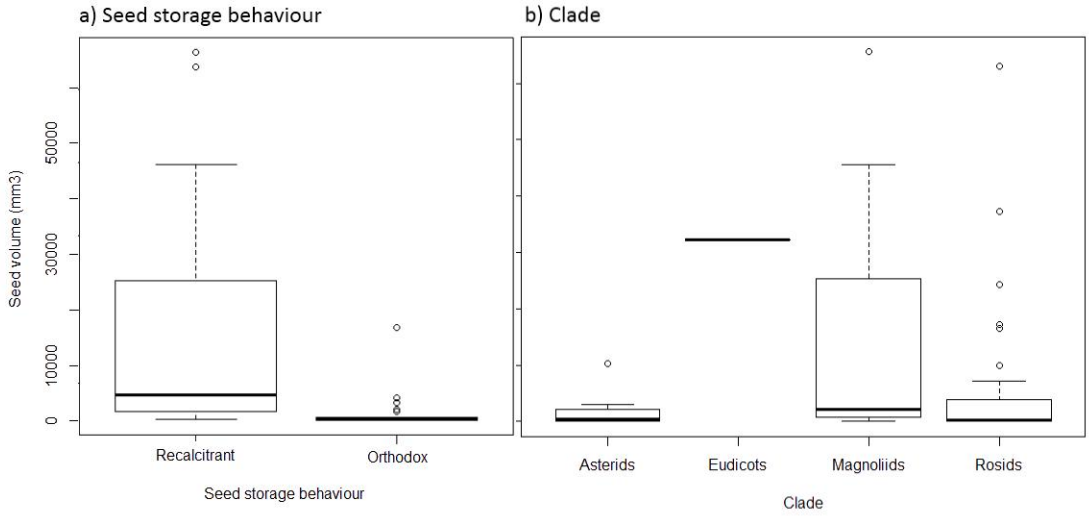


Figure 6.3: Seed volume in categories of a) seed storage behaviour and b) Clade for 54 species of tree found in Doi Suthep-Pui national park.

Recalcitrant species had higher germination rates in full shade than in partial shade (median Shade GR:Sun GR =1.40), and the opposite was true of orthodox species (Shade GR :Sun GR =0.718), ($p=0.001$), (Table 6.3).

Table 6.3: Comparison of seed and germination characteristics for 54 species of tree found in Doi Suthep-Pui National Park by seed storage behaviour. Mann-Whitney test used for comparison of mean. Shade GR:Sun GR refers to the ratio of germination rate when seeds are germinated in full shade to that when they are germinated in partial shade. IQR – Interquartile range.

		Orthodox			Recalcitrant			MW
Trait	Units	median	IQR	N	median	IQR	n	Sig.
Seeds in diaspore	count	4	19	30	1	0	24	**<0.001**
Seed Dry Weight	g	0.018	0.045	29	0.67	1.721	21	**<0.001**
Seed Volume	mm^3	130	362	30	4521	22996	24	**<0.001**
Seed internal volume	mm^3	123	340	27	3955	22705	23	**<0.001**
Shade GR:Sun GR	Ratio	0.718	0.399	30	1.040	0.329	24	**0.001**

6.3.2. Predicting germination rate

Six species (*Helicia nilagirica* - S104, *Sarcosperma arboreum* - S105, *Aglaia lawii* - S123, *Machilus bombycina* - S163, *Markhamia stipulata* - S204 and Cinnamomum caudatum - S207) had higher germination (at least 25% higher) in full shade than in partial shade. Of these only one (*Markhamia stipulata* - S204) was orthodox. Seven species (*Diospyros glandulosa* - S012, *Prunus cerasoides* - S071, *Ficus semicordata* - S315, *Erythrina subumbrans* - S317, *Lithocarpus fenestratus* - S337, *Ficus racemosa* - S365 and Ficus heteropleura - S372) had between 25% and 100% higher germination in partial shade than in full shade (Fig. 6.4). Of these, only one (*Lithocarpus fenestratus* - S337) was recalcitrant. Thirteen species had germination rates in partial shade over twice that in full shade. Ten of these species were orthodox (*Melia toosendan* - S005, *Macaranga denticulata* - S009, *Balakata baccata* - S015, *Acrocarpus fraxinifolius* - S031, *Ficus subulata* - S039, *Betula alnoides* - S048, *Gmelina arborea* - S078, *Eurya acuminata* - S086, *Callicarpa arborea* - S156 and *Ficus superba* - S368), and were analysed as a separate group "Light-preferring" when considering relationships to growth and survival (Fig. 6.4).

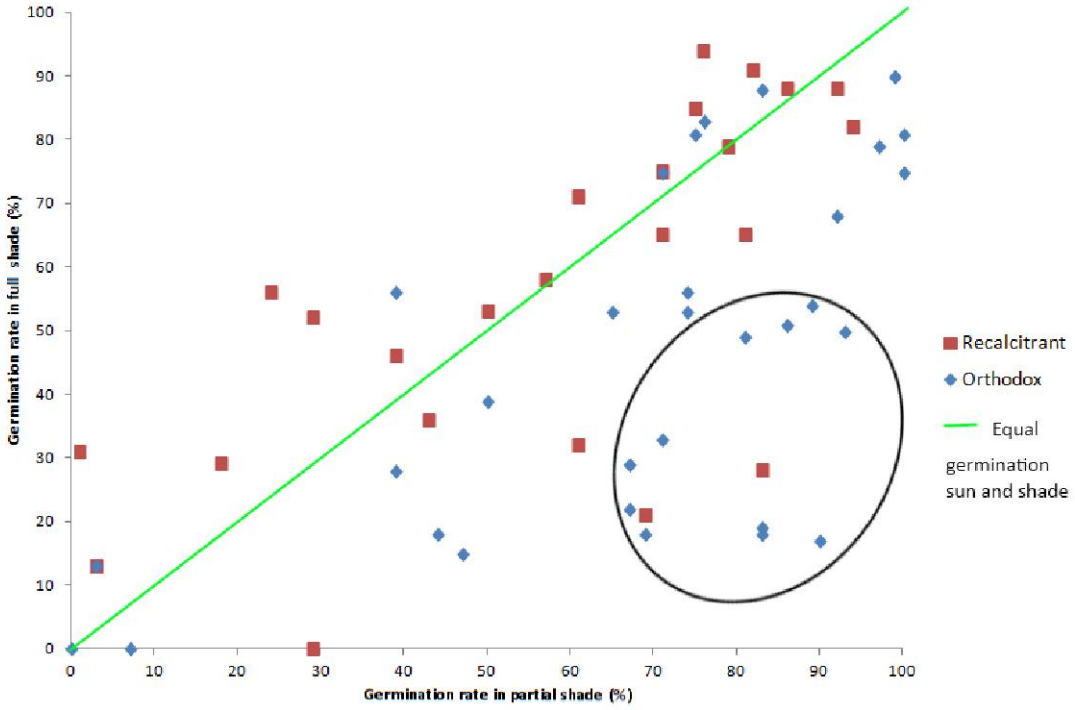


Figure 6.4: Correlation of germination rates in full shade and partial shade for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand. Species where germination is far higher in the partial shade than full shade are encircled.

6.3.3. Differences based on seed storage behaviour and light preference

No significant differences in seed size or functional thickness were found between light-preferring orthodox species and other orthodox species. However, this may be due to the small number of species considered (10 species of orthodox light-preferring species only), as clear differences can be observed in seed size (Fig. 6.5).

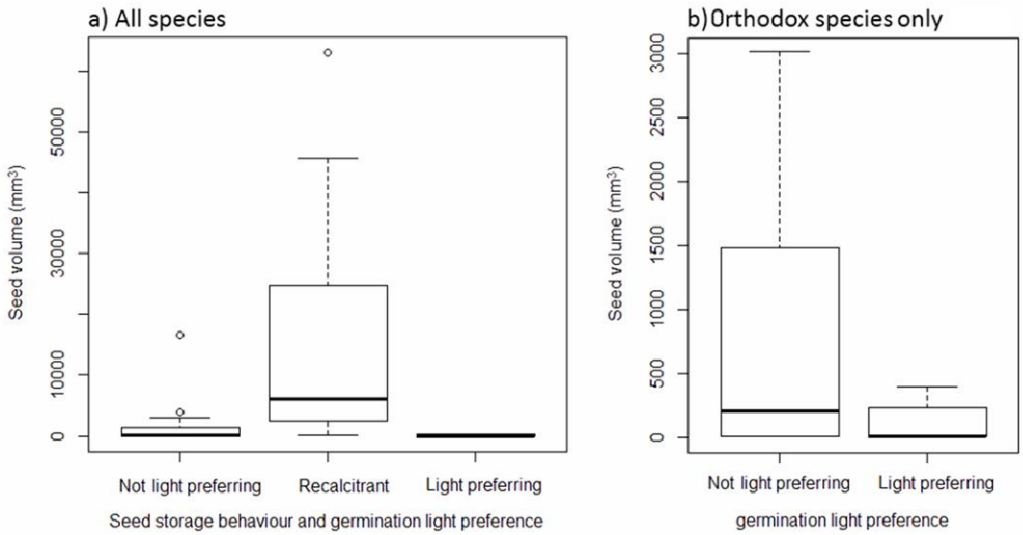


Figure 6.5: Seed size (volume) in 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand. Both charts show both light-preferring and non-light-preferring species, but b) is shown at a larger scale to demonstrate differences between the two.

Seed coat thickness, MLD and germination ranges were similar between groups. In orthodox species, Sun GR was correlated negatively with seed size. When non-light-preferring species were considered alone, this relationship became even more pronounced, but did not occur within light-preferring species. In recalcitrant species only, Shade GR was correlated positively with seed size. MLD in full shade was positively correlated with functional thickness in orthodox species that were not in the light-preferring group. Seed germination asynchrony (Range) was related to functional thickness in orthodox species that preferred light for germination. Shade GR :Sun GR was correlated positively with seed size, however, when orthodox and recalcitrant species were investigated separately, no relationship was found (Table 6.4).

Table 6.4: Correlations of seed characteristics and germination performance for 54 species of tree from Doi Suthep-Pui National Park. Seedlings were germinated in both full and partial shade; germination rate (GR), median length of dormancy (MLD) and range of germination (range) were assessed. The ratio of shade germination rate over sun germination rate was also measured. Species are divided into orthodox and recalcitrant species. Significant values are marked in bold.

Seed trait	Sun GR	Shade GR	MLD Sun	MLD Shade	Range Sun	Range shade	Shade GR: Sun GR
Recalcitrant species (n24)							
Seed Volume	0.332 (0.057)	0.404* (0.025)	-0.198 (0.177)	0.015 (0.472)	-0.261 (0.109)	-0.264 (0.106)	0.164 (0.221)
Functional thickness	-0.186 (0.198)	-0.167 (0.224)	-0.038 (0.432)	-0.084 (0.351)	-0.118 (0.296)	-0.068 (0.379)	-0.045 (0.42)
All orthodox species (28)							
Seed Volume	-0.348* (0.032)	-0.094 (0.314)	-0.013 (0.473)	0.062 (0.375)	-0.16 (0.204)	0.227 (0.118)	0.124 (0.262)
Functional thickness	-0.313 (0.059)	-0.221 (0.139)	-0.085 (0.34)	0.258 (0.101)	-0.282 (0.081)	**0.470** (0.008)**	-0.080 (0.349)
Orthodox seeds - light preferred for germination (n=10)							
Seed Volume	-0.110 (0.381)	-436 (0.104)	-0.049 (0.447)	-0.309 (0.192)	-0.116 (0.375)	0.261 (0.233)	-0.353 (0.159)
Functional thickness	0.157 (0.356)	-0.127 (0.383)	-0.536 (0.085)	0.108 (0.400)	-0.572 (0.069)	0.705* (0.025)	-0.241 (0.283)
Orthodox seeds - light not preferred for germination (n=18)							
Seed Volume	**-0.624** (0.002)**	-0.338 (0.079)	0.066 (0.395)	0.265 (0.136)	-0.224 (0.178)	0.133 (0.293)	0.061 (0.402)
Functional thickness	-0.414 (0.044)	-0.109 (0.334)	0.265 (0.136)	**0.479* (0.022)**	-0.147 (0.281)	0.376 (0.062)	-0.099 (0.348)

6.3.4. Predicting growth rate in the nursery

Nursery growth rates were not significantly different between orthodox and recalcitrant species or between light-preferring orthodox species and other groups. However, the range of growth rates for orthodox species was much larger than that for recalcitrant species and was skewed towards faster growing species (Fig. 6.6).

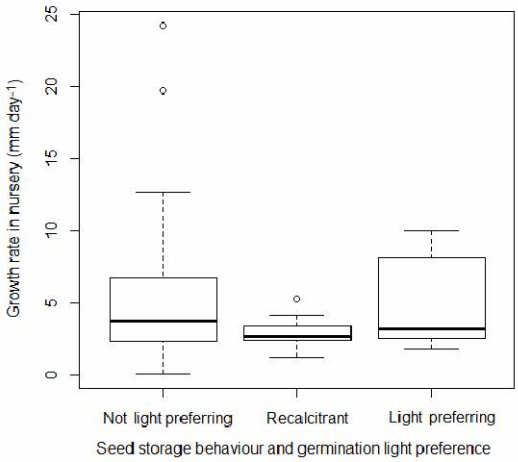


Figure 6.6: Nursery growth rates for orthodox species preferring light for germination, recalcitrant species and orthodox species not preferring light for germination for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand and raised as part of a reforestation project by the Forest Restoration Research Unit (FORRU).

Nursery growth rate was unrelated to any seed or germination measure in recalcitrant seeds. In orthodox seeds that do not prefer light for germination, growth was positively correlated with all measures of seed size and with functional thickness. Within light-preferring species, nursery growth rate was correlated with seed volume (Table 6.5).

Table 6.5: Correlations of seed characteristics with nursery growth rate for 53 species of tree from Doi Suthep-Pui National Park. Species are divided into recalcitrant species, orthodox species that had higher germination in full sun than in partial shade and orthodox species that had similar germination rates in both full sun and partial shade. Significant values are marked in bold.

Seed characteristic	Units	Recalcitrant (n=22)	Light preferred (n=10)	Light not preferred (n=18)
Seed mean diaspore	Count	-0.024 (0.458)	-0.138 (0.362)	**-0.552** (0.007)**
Seed external volume	mm^3	-0.132 (0.280)	**0.828** (0.003)**	**0.621** (0.002)**
Seed coat thickness	µm	0.304 (0.090)	0.158 (0.368)	0.533* (0.011)
Functional thickness	µm	0.246 (0.141)	**0.778* (0.020)**	**0.722*** (<0.001)**
Seed internal volume	mm^3	-0.123 (0.297)	**0.857** (0.007)**	**0.591** (0.005)**
Sun GR	percentage	-0.111 (0.312)	0.286 (0.228)	-0.484* (0.018)
Range shade	days	-0.31 (0.080)	0.600* (0.044)	0.421* (0.036)

6.3.5. Growth – first growing season after planting (two weeks to five months)

The relationships between nursery growth rates and field growth rates in both the first and the second year after planting were investigated. As *Melia toosendan* (S005) was an outlier, with a field growth rate double that of other species, it was therefore excluded from the analysis.

Growth rates in the first season after planting varied significantly between species and between plots. In some cases, growth in the first season was up to 70% of that in the second season and in others, seedlings actually lost height over the first growing season. Growth in the 2001 plots as a proportion of growth in the second year after planting was lowest, with growth of only 16 % that of the second year. It was highest in the 2000 plot where growth in the first season after planting was over a quarter of that in the second season (Table 6.6)

Table 6.6: Growth in the first season after planting as a proportion of that during the second season after planting for 53 species of tree from Doi Suthep-Pui National Park, raised in the nursery and planted as part of a restoration project in 1998, 1999, 2000 and 2001.

Year	Median	Interquartile Range (IQR)	Minimum	Maximum
1998	0.151	0.188	-0.351	0.558
1999	0.198	0,186	-0.442	0.695
2000	0.259	0.222	-0.017	0.563
2001	0.159	0.155	-0.158	0.398

In the 1998 plots, non-light-preferring orthodox species had the fastest growth, followed by recalcitrant species and finally light preferring species. In the 1999 and 2000 plots, performance was similar between groups. In the 2001 plot, both groups of orthodox species performed better than recalcitrant species (Fig. 6.7)

In the 2000 plot, in orthodox, non-light-preferring species, there were positive correlations between first season growth and both seed internal volume and functional seed coat thickness ($p=0.010$ and $p=0.006$ respectively). In the 1999 plot, in orthodox, non-light-preferring species, there was a positive correlation between growth and germination rate in the shade ($p=0.008$).

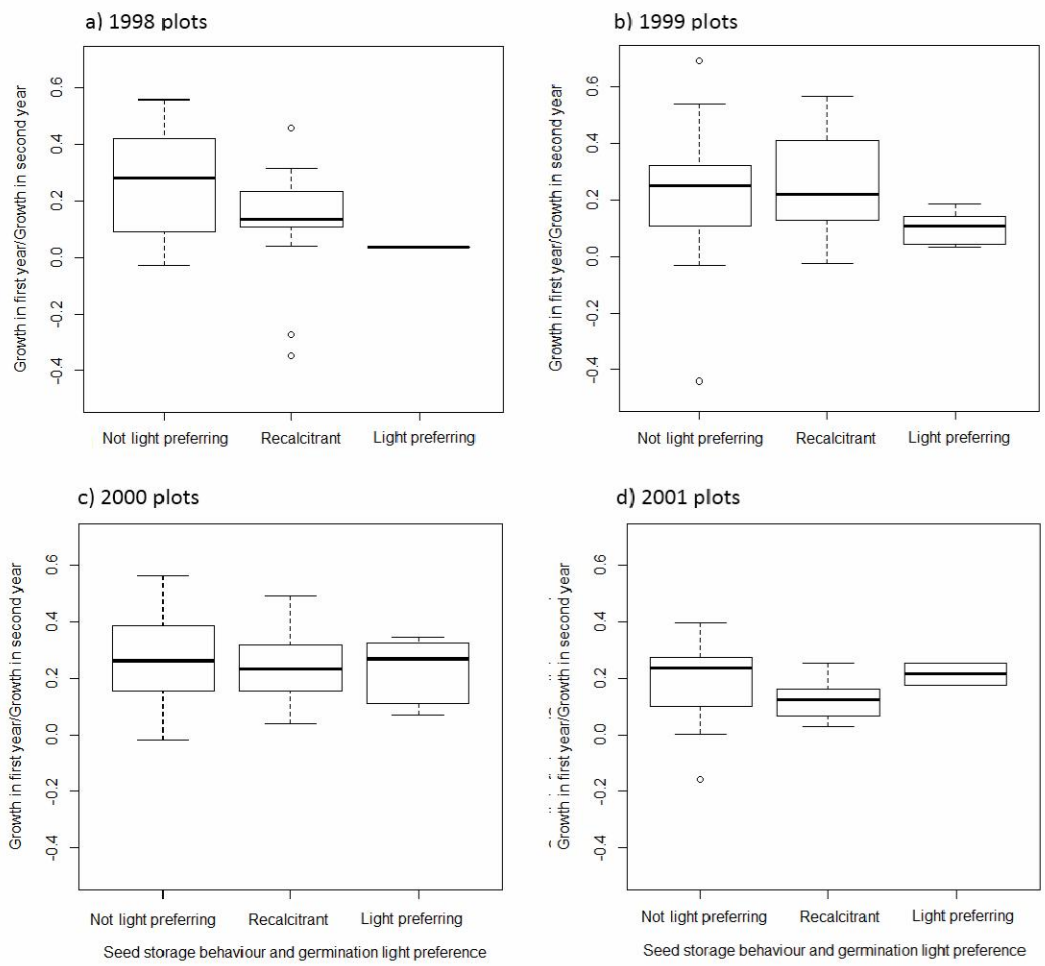


Figure 6.7: Growth rates in the field over the first growing season after planting out as a proportion of growth during the second season for orthodox species preferring light for germination, recalcitrant species and orthodox species not preferring light for germination for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand and planted as part of a reforestation project by the Forest Restoration Research Unit (FORRU). Measurements are provided for species planted in a) 1998, b) 1999, c) 2000 and d) 2001.

6.3.6. Growth– second growing season after planting (five to seventeen months)

Growth was faster for species with orthodox seeds in all except the 2001 plot. Whilst the growth of recalcitrant species was similar in each plot (about 50 cm), large differences were seen in orthodox species, with fastest growth in the 1999 and slowest in the 2001 plot, where it was similar to that of recalcitrant species. No difference was found between light-preferring and non-light-preferring orthodox species in any plot; although the mean growth rate of the two orthodox groups changed considerably between plots, they differed in similar manner to each other (Fig. 6.8). In all except the 1999 plots, for non-light-preferring orthodox species, growth rate during the second season after planting was correlated negatively with shade germination rate (1998 p=0.009, 2000 p=0.008, 2001 p=0.001).

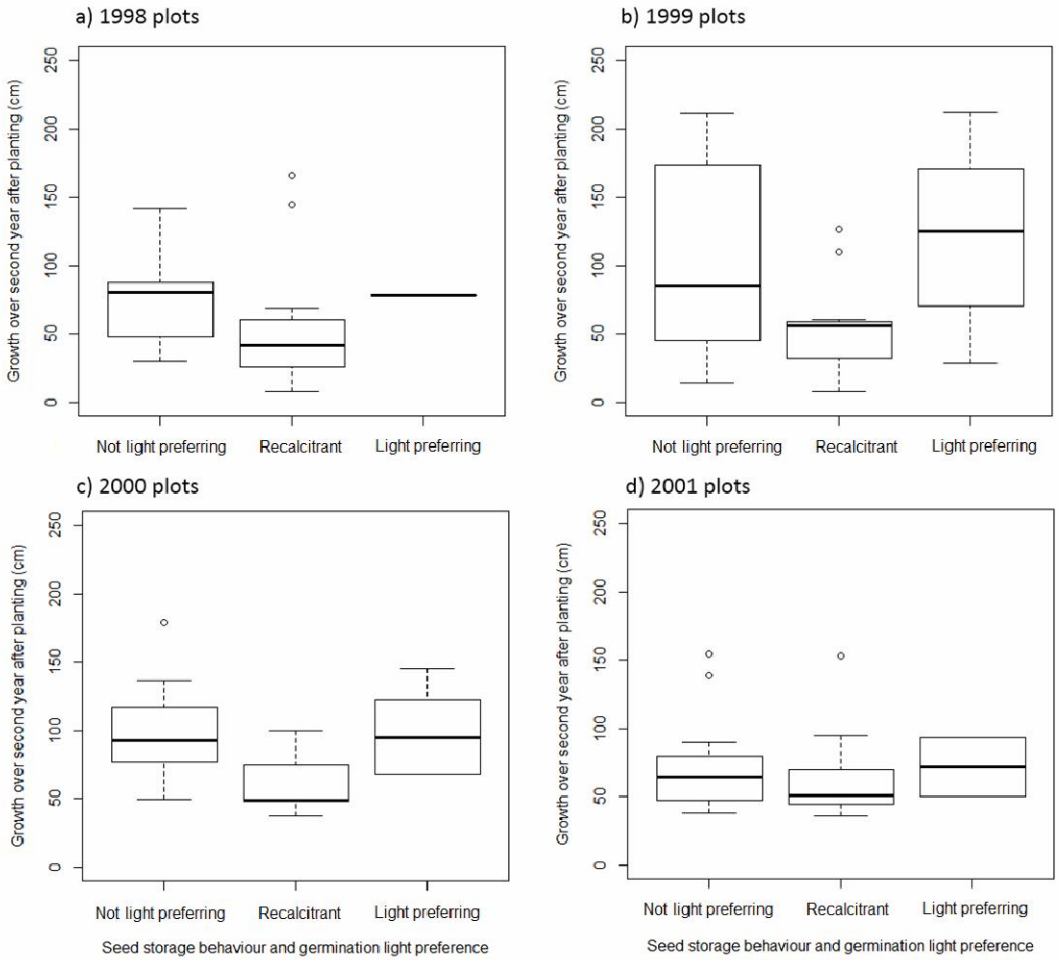


Figure 6.8: Growth rates in the field over the second growing season after planting out for orthodox species preferring light for germination, recalcitrant species and orthodox species not preferring light for germination for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand and planted as part of a reforestation project by the Forest Restoration Research Unit (FORRU). Measurements are provided for species planted in a) 1998, b) 1999, c) 2000 and d) 2001.

6.3.7. Survival – first growing season after planting (two weeks to five months)

Survival over the first year after planting was much lower in the 1999 plots than in other years. Although all groups were affected, the non-light-preferring orthodox species were affected by the lower survival rate less than the other two groups (Fig. 6.9). In orthodox species that were non-light-preferring, survival over the first growing season in the 1999 plot was negatively correlated with seed size (p=0.008).

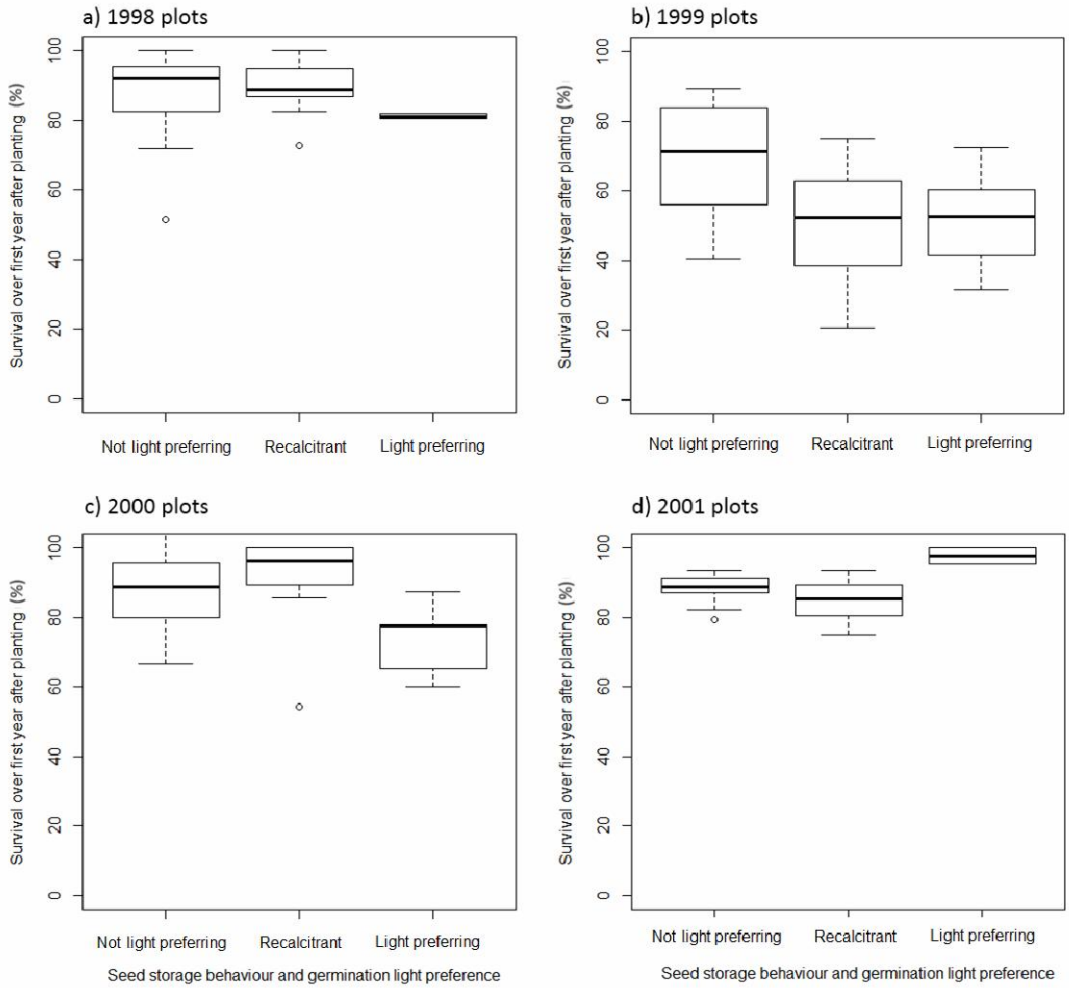


Figure 6.9: Survival rates in the field over the first growing season after planting out for orthodox species preferring light for germination, recalcitrant species and orthodox species not preferring light for germination for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand and planted as part of a reforestation project by the Forest Restoration Research Unit (FORRU). Measurements are provided for species planted in a) 1998, b) 1999, c) 2000 and d) 2001

6.3.8. Survival – second growing season after planting (five to seventeen months)

Survival over the second year, which included the dry season, varied significantly between plots. Survival in the 1999 plots was lower for all species groups than in the 1998 plots. Survival in the 1998 and 1999 plots was lower for species that germinated more effectively under partial shade conditions. In the 2000 plots, recalcitrant species had low survival and in the 2001 plots, all groups survived equally well (Fig. 6.10).

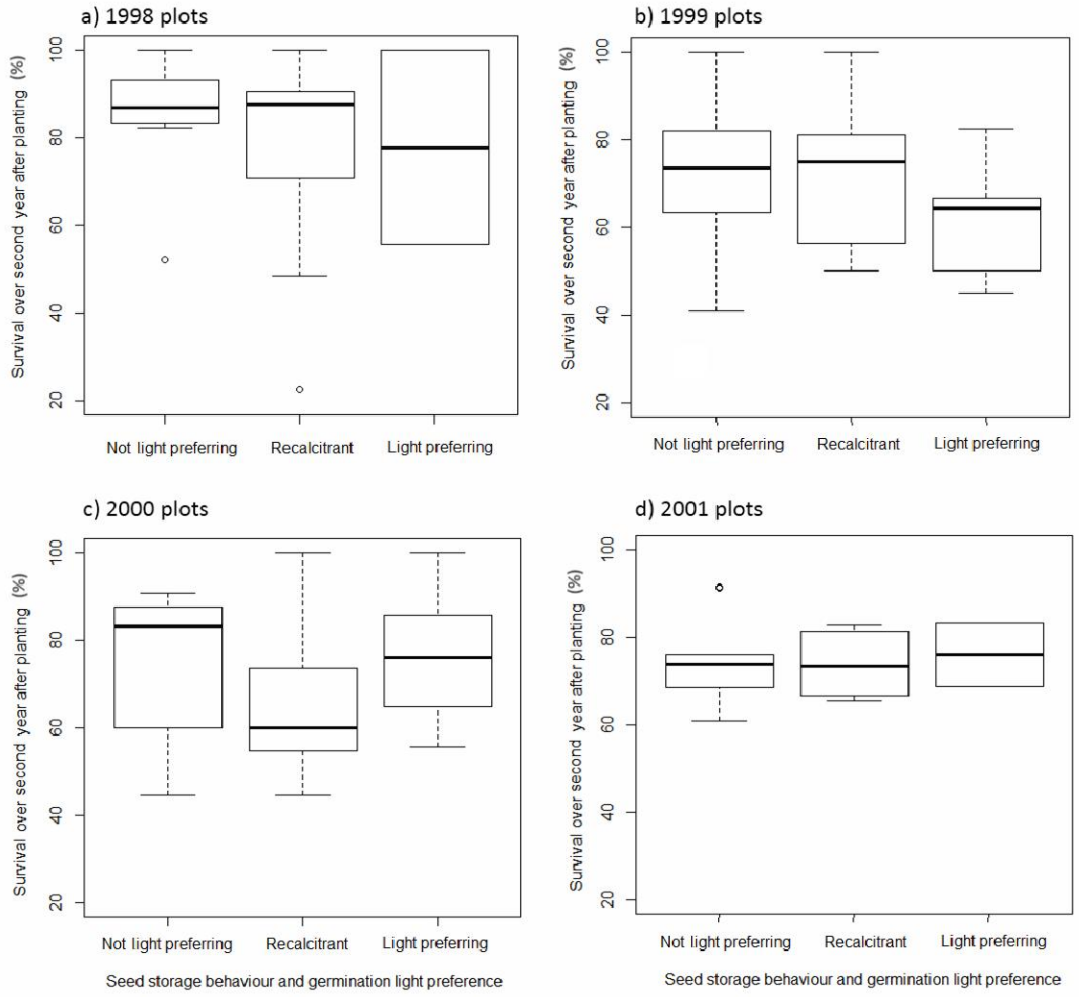


Figure 6.10: Survival rates in the field over the second year after planting out for orthodox species preferring light for germination, recalcitrant species and orthodox species not preferring light for germination for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand and planted as part of a reforestation project by the Forest Restoration Research Unit (FORRU). Measurements are provided for species planted in a) 1998, b) 1999, c) 2000 and d) 2001.

6.3.9. Fruiting phenology

Dry fruits distributed by animals ripened during the wet season from June to November. Dry fruits distributed by wind ripened primarily around March. Fleshy and Juicy fruits ripened throughout the year but primarily during the mild season from December to March, whereas fruits identified as slightly-fleshy ripened all year round (Fig. 6.11).

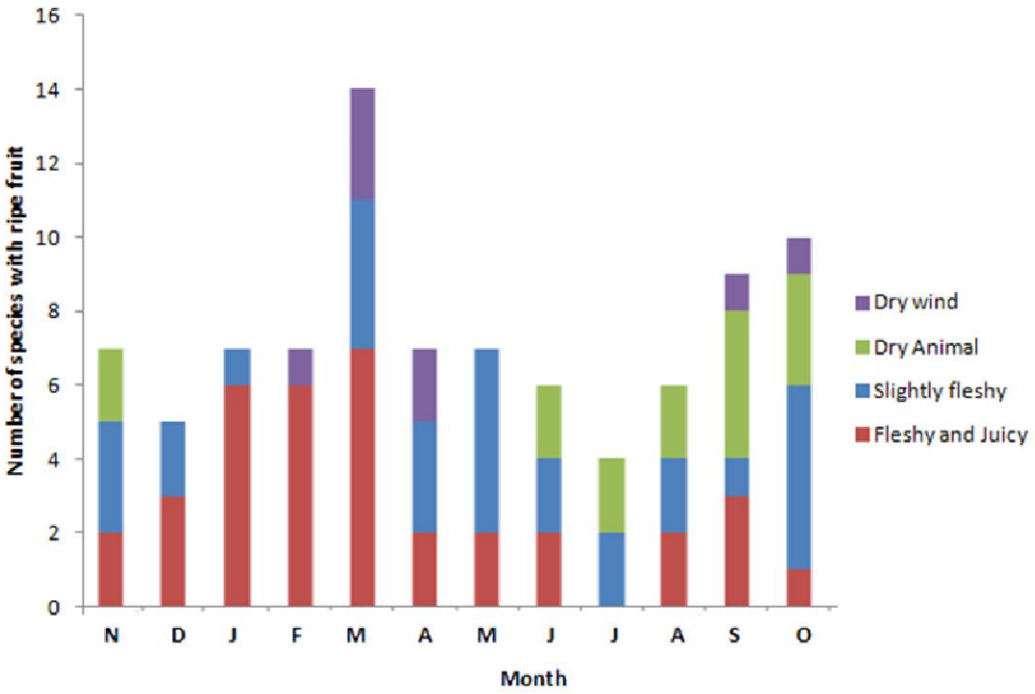


Figure 6.11: Fruiting phenology for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand separated by fruit fleshiness category and seed dispersal type.

No fruit of species with recalcitrant seeds fell in December, January or February. Orthodox species fell in all months of the year except for May, peaking in December to March and being lowest in July. Seed size was strongly linked to fruiting month, with the largest seeds being dropped from April to June. As the largest seeds were all recalcitrant, there was also an increase of recalcitrant and hypogeal germinated species at this time. However, it is worth noting that smaller recalcitrant species fell over a much broader period, from February to September (Fig. 6.12)

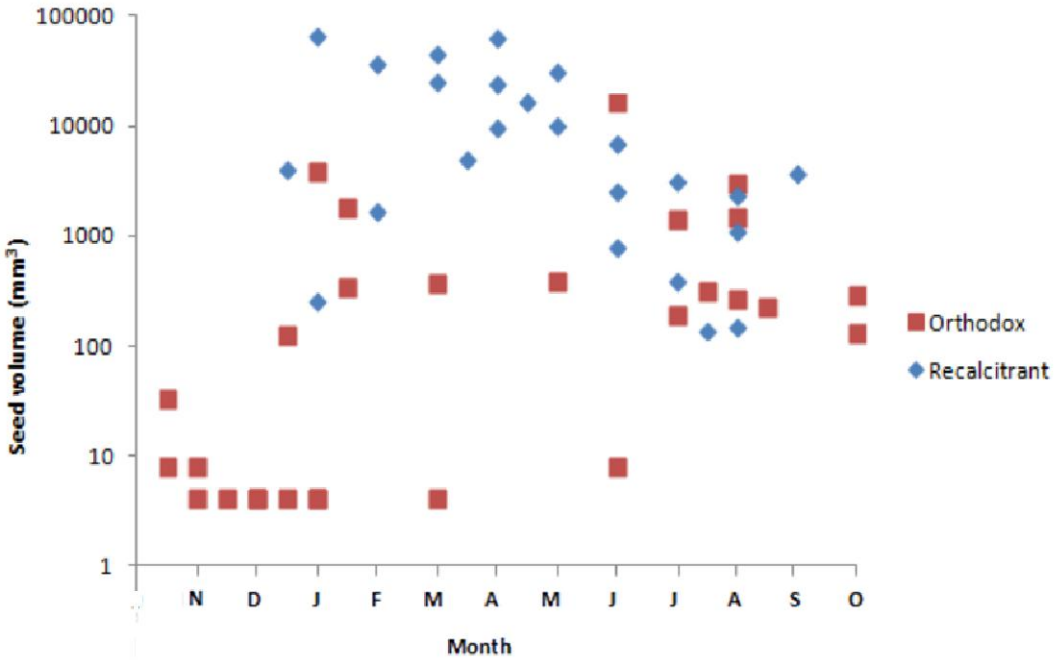


Figure 6.12: Fruiting phenology for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand considered by seed size and seed storage behaviour. Please note that for the sake of clarity, the months run from November to October.

The relationship between fruiting month and median length of dormancy (MLD) for recalcitrant species was stronger than that for orthodox species which, apart from a small number of outliers had a less variable MLD than recalcitrant species. In recalcitrant species, the MLD for species ripening in August to October was much longer than for species that ripened in January. For recalcitrant species, MLDs combined with fruiting month would cause species to germinate in April, the start of the wet season (Fig. 6.13).

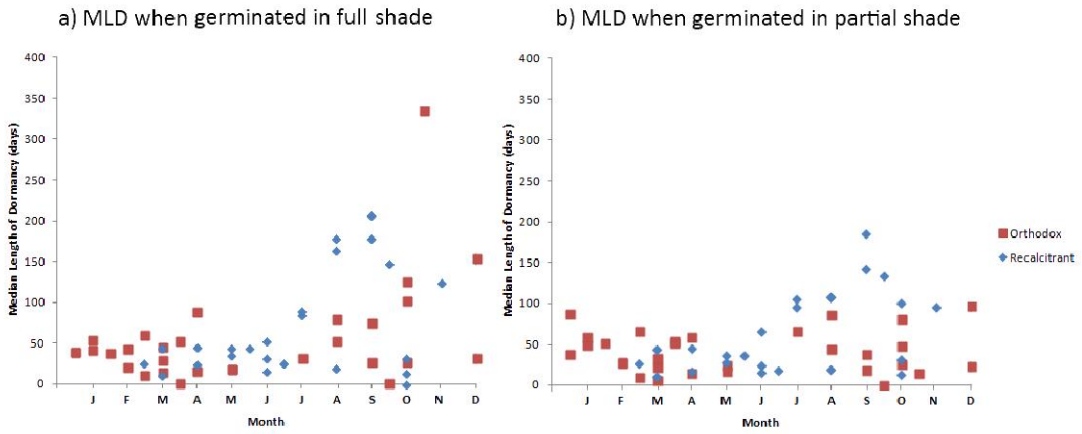


Figure 6.13: Days from planting to the germination of the median seed (MLD) for 54 species of tree found in Doi Suthep-Pui National Park in Northern Thailand and raised as part of a reforestation project by the Forest Restoration Research Unit (FORRU) considered by size and seed storage behaviour.

6.4. Discussion

The relationships among fruit, seed and germination traits of 54 species of tree from the seasonally-dry tropical forest of northern Thailand were investigated to see how they related to each other, and whether they predicted performance in both the nursery and field for restoration purposes. Whilst seed dry weight has been used as a functional trait in many studies (Fenner 1983; Choe *et al.* 1988; Negi & Todaria 1997; Aud & Ferraz 2012; Hill, Edwards & Franks 2012), here seed volume, was found to be an excellent alternative, especially as it can be derived from herbarium specimens when weight measurements are difficult to obtain.

6.4.1. Relationship between seed traits

The strong correlation found here between clade and seed size and the combined effect of both clade and seed size on seed storage behaviour are in line with findings that these traits are conserved characteristics (Lord, Westoby & Leishman 1995; Moles *et al.* 2005). The covariance of seed storage behaviour, seed size and germination type was also in keeping with predictions that large seeds will tend towards desiccation intolerance (Dickie & Pritchard 2002; Daws, Garwood & Pritchard 2005), and hypogeal germination (Garwood 1996; Ibarra-Manriquez, Ramos & Oyama 2001; Zanne, Chapman & Kitajima 2005).

6.4.2. Effects of seed characteristics on germination in differing light

Recalcitrant species, which are more prone to desiccation than orthodox species, tended to germinate better in the full shade than in the partial shade treatment. This supports the theory that germination rate of recalcitrant seeds may be higher in shade due to the higher risk of desiccation in sunlight (Augspurger & Kelly 1984). Also, the netting placed around the shade treatment may have helped to retain humidity and soil moisture around the seeds. Alternatively, it may be linked to temperature differences caused again but the dark netting as both increased temperature and diurnal variations in temperature have been found to affect germination rates (Aud & Ferraz 2012). It is interesting to note that this occurred in a nursery setting where seeds were well supplied with water on a daily basis. It may

be valuable to investigate the soil moisture levels nursery more closely, and to consider watering twice daily or the provision of an under-tray watering system. It may also be valuable to consider germination under full shade as a way of increasing the germination rate of recalcitrant species.

Species which had higher germination rates in partial shade than in full shade were identified. This appears to support the theory of a photoblastic mechanism (Pearson *et al.* 2003). That they were mostly very small orthodox seeds is in line with the pioneer concept (Swaine & Whitmore 1988). However, some germination occurred in full shade for all species with a preference for partial shade germination. Whilst this could be due to sun-flecks, it is not possible to discount the possibility that this increase in germination in partial shade was due to a reduction in “damping off” (Taher & Cooke 1975). The “damping off theory” was supported by the existence of two recalcitrant, hypogeal species that had a higher germination ratio in partial shade (*Heynea trijuga* - S157 and *Lithocarpus elegans* - S280), as recalcitrant species are unlikely to exhibit photoplastic germination. Alternatively, it has been found that some species usedirurnal temperatuer variations to identify breaks in the canopy (Kos & Poschlod 2007; Gonzalez-Rivas *et al.* 2009;). A more controlled experiment involving a number of different light, temperature and humidity conditions and the application of fungicide may allow the mechanisms involved to be identified.

Here, non-light-preferring orthodox species displayed a negative correlation between seed size (and functional thickness) and germination rate. However, in recalcitrant species, there was a positive correlation between seed size (but not functional thickness) and germination rate. The increased germination rate in recalcitrant species (which are larger than orthodox species) supports the theory of higher germination in seeds with higher maternal investment (larger seeds) (Westoby *et al.* 2002). However, the reason for the higher germination rates in smaller orthodox seeds is unclear and requires further work with a larger number of species. One hypothesis might be that greater dormancy breaking methods are needed in species with thicker seed coats or other protective coverings.

6.4.3. "Light-preferring" seeds

Here, a preference for open conditions for germination did not confer faster growth in the nursery, faster growth in the field, or greater field survival. If light preference in germination is taken as a diagnostic identifier of pioneer species, these results do not support the predicted fast growth of pioneer species (Leishman & Westoby 1994a). However, if a broader identification of pioneers being linked to orthodox seeds is used, there is evidence to support this theory (see below).

6.4.4. Effects of seed characteristics on nursery growth

Smaller-seeded, epigeal species may initially grow slower than larger, hypogeal species due to reduced metabolic reserves (Foster & Janson 1985; Kitajima 1996; Westoby, Leishman & Lord 1996; Kisdi & Geritz 2003), but may overtake species with hypogeal germination quickly due to their ability to respond more quickly to light availability (Kitajima 1994; Paz & Martinez-Ramos 2003; Baraloto, Forget & Goldberg 2005; Poorter & Rose 2005). The nursery growth rates found here generally supported the second assertion, as orthodox species showed faster nursery growth. However, as detailed growth rates over the period in the nursery were not available, it is not possible to assess whether larger, hypogeal seeds grew faster initially. Consideration of recalcitrant species on their own do not show a link between seed size and nursery growth rate, but within orthodox species, where almost all seeds showed epigeal germination, there was evidence of faster growth with this higher maternal investment (Westoby *et al.* 2002). Measurement of nursery growth over a shorter timescale may also shed light on these relationships.

6.4.5. Effects of seed characteristics on field growth

Both growth in the nursery and that in the field in both years after planting were greater in orthodox than recalcitrant species and this was reflected in the correlation between nursery and field growth rates in three of the four plots, the exception being the 2000 plot. Growth in the 2000 plot was no slower than other years and there were no indications of differences in species planted that may shed light on this. Further investigation of other species characteristics, such as leaf traits may be valuable.

6.4.6. Effects of seed characteristics on field survival

No links between either germination type or seed size with survival in the field were found. As larger, hypogeal species were not found to have greater survival, there was no evidence for the increased sprouting ability of larger hypogeal seeds (the reserve effect), (Armstrong & Westoby 1993; Westoby, Leishman & Lord 1996) or the 'metabolic effect' hypothesis (Westoby, Leishman & Lord 1996; Leishman *et al.* 2000). As all species were planted out at a similar size, the seedling size effect (Dalling, Harms & Aizprua 1997; Dalling & Harms 1999; Green & Juniper 2004) would not be expected to occur here. Conversely, as no link between survival of smaller, orthodox seeds, or species with higher germination in partial shade, there was no support for the pioneer hypothesis that suggests that species with smaller seeds would be better adapted for the drought conditions found during restoration (Bazzaz 1991; Leishman & Westoby 1994b; Whitmore 1998).

6.4.7. Phenology of fruiting and germination

Support was found for the seasonality of orthodox and recalcitrant seeds, with orthodox species fruiting more during December to March (the dry season) and recalcitrant species only falling during the mild and wet season when the risk of desiccation was reduced (Ray & Brown 1995; Daws, Garwood & Pritchard 2005; Daws, Garwood & Pritchard 2006), in contrast with findings in the Australian tropics where no such relationship was found (Hill & Edwards 2010). A predicted peak of fruiting was found (Garwood 1983) just before the rainy season. However, fruiting of some recalcitrant species occurred at all times of year supporting the supposition that phenological timing is not a strong selection factor (Hill, Edwards & Franks 2012). Germination was found to be timed primarily during the rainy season (Garwood & Olive 1982; Garwood 1983) which suggests germination is timed to ensure maximum survival. No support was found for Garwood's other finding (1983) that pioneer species tended to germinate early in the wet season as all species tended to germinate at the beginning of the rainy season. However, here, germination was performed in the nursery and triggers for germination were not considered. It is possible that the timing of germination in the field, triggered by

rainfall, may support the prediction and further, field-based trials may be valuable. The predicted correlation between seed size and MLD (Daws *et al.* 2007; Paine & Beck 2007; Hautier *et al.* 2010) was not supported in either recalcitrant or orthodox species or by considering both recalcitrant and orthodox species together. This would suggest that seed predation is not an important limiting factor for seed size within this environment. Furthermore, no difference in the length of time to germination was found between desiccation-tolerant and intolerant species, despite the predicted shorter germination period for desiccation-intolerant species to reduce the risk of desiccation (Pammenter & Berjak 2000; Pritchard *et al.* 2004).

Wind-distributed species fruited mainly in March. As the highest annual wind speeds occur in April (Information Services - Thai Meteorological Office-personal communication 2013) when gusts can reach 20m per second, this timing allows for the maximum dispersal of wind-dispersed seeds. This timing may also be linked to the relatively open canopy at this time of year

Animal-dispersed fruits were produced all year round, but there were distinct phenological differences based on the moisture levels within the fruit, with dry fruits mainly in the wet season (June-November), fleshy and juicy fruits in the mild season (December-March) and species defined as “slightly fleshy” occurring at all times of year. Due to the small number of species available, the lack of data on specific animal dispersers and the biases inherent in the selection of these species for the restoration project it is difficult to draw any conclusions from these data. However, it is worth noting that dry fruits, which often rely on seed burying behaviours for dispersal, occurred during the wet season when fruit is in abundance and storage may be a valuable for the animals, and that fleshy fruits occur during the period of lowest rain, potentially using their water content as an additional attraction to frugivores. Larger seeds were dropped in April to June. This seasonality, combined with dormancy period does not support the prediction that large-seeded species tend towards faster germination (Louda 1989; Blate, Peart & Leighton 1998). The reasons for this difference should be considered more fully with a broader range of species.

6.4.8. Conclusions and Implications of for restoration schemes

Seed and germination characteristics have strong implications for the choice of species for forest restoration schemes broadly in keeping with predictions from earlier studies. The differing patterns of germination, growth and survival in orthodox and recalcitrant species suggest that species of these types should be considered separately in future studies of performance as they have implications beyond that of seed size. In general, orthodox species show faster growth and are more suited to restoration projects and nursery growth rates are good predictors of later performance.

The identification of pioneer species purely on the basis of seed germination, however, was not found to be useful in predicting growth or performance in either the nursery or the field as performance of seeds that germinated more effectively in partial shade was indistinguishable from that of other orthodox species. A broader interpretation of the pioneer concept, where traits other than seed traits were used may prove valuable and would be a useful area of further research.

7. Predictions of growth rates in a seasonally-dry forest restoration project using phenological leafing strategy, wood and leaf traits

7.1. Introduction

7.1.1. Background

Identifying species that will grow effectively in forest restoration schemes often requires time-consuming and expensive field trials from which results are not available for several years (Elliott *et al.* 2002; Elliott *et al.* 2003). The Forest Restoration Research Unit (FORRU) of Chiang Mai University have been running nursery and field trials in the Doi Suthep-Pui National Park since 1997 (Elliott *et al.* 2002; Elliott *et al.* 2003) based around the Framework Species Approach to forest restoration. These have been very successful (Blakesley *et al.* 2002; Elliott *et al.* 2002; Elliott *et al.* 2003) but it has been suggested that these trials may be targeted more effectively by pre-assessing species using easily measured physical, chemical and life-history traits (Walters & Reich 1999; Poorter & Bongers 2006).

Functional traits have been found to be useful predictors of growth and survival (Westoby *et al.* 2002; Reich *et al.* 2003; Wright *et al.* 2010) and specifically in seasonally-dry tropical forest (Chaturvedi, Raghubanshi & Singh 2011) and restoration projects (Pywell *et al.* 2003). Species with low leaf specific area and denser wood have been found to grow slower than those with high specific leaf areas and less dense wood (Wright *et al.* 2010). Other authors however have found that hydraulic architecture is a better predictor of growth rates than robustness in the form of wood or leaf density (Zhang & Cao 2009; Fan *et al.* 2012).

A great deal of work has been done on identifying relationships between leaf traits and a number of key relationships and tradeoffs have been found (Wright *et al.* 2004). Increasingly, similar relationships between wood traits (Chave *et al.* 2009) have also been identified. Here, key leaf traits, (see Chapters 3) in the seasonally-dry tropical forest of northern Thailand have been found to correlate as predicted within a single leaf economic spectrum (Wright *et al.* 2004; Chave *et al.* 2009). Wood traits have been found to vary on three different axes (see chapter 4).

7.1.2. Hypotheses and aims

Here, the extent to which wood and leaf traits are linked to species growth rates is as yet unknown. The validity of using wood and leaf trait data to predict growth rates for plantation seedlings in the seasonally-dry, tropical forest of northern Thailand was tested , and models created that may be used as predictors of growth in the field. It was predicted that;

- Species with leaves at the “biomass retention” end of the leaf economic spectrum will grow more slowly than those at the “biomass gaining” end.
- Species with dense wood will grow more slowly than those with less dense wood
- Species with high levels of protective features, such as drought tolerance traits, in either wood or leaves. will grow slower than those with few protective features.
- Species with wide xylem vessels will grow faster than those with narrow xylem vessels

7.2. Methods

7.2.1. Doi Suthep-Pui National Park

The Doi Suthep-Pui National Park (created in 1981) is an area of approximately 260 km^2 of seasonally-dry tropical forest near Chiang Mai in Northern Thailand (18.83203°N / 98.88805°E) and ranges from 340 to 1680m a.s.l (Maxwell & Elliott 2001). Whilst annual rainfall is high, rainfall in January and February can be as low as 6 mm a month, rising after the start of the monsoon in April or May to a peak of 275mm in August before dropping swiftly from October. The dry season is sub-divided into the cool-dry season (November–January) where maximum temperatures range from 30 °C to 32 °C and the hot-dry season (February– April), with a maximum temperature daily temperature of between 30 °C and 39 °C (Fig. 7.1.). Whilst previously fully forested, the area has experienced serious forest loss and degradation with approximately 50% of the park deforested in 1996 (Elliott *et al.* 2003)

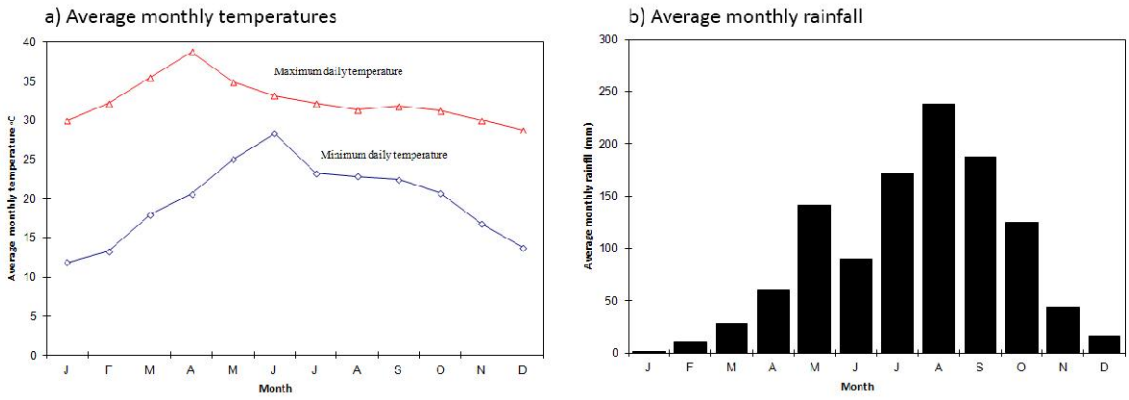


Figure 7.1: Monthly (a) maximum and minimum daily temperature and (b) rainfall in the Chiang Mai area of northern Thailand. Based on records from between 1952 and 1997– (Maxwell & Elliott 2001)

7.2.2. Species selected

Species used here consisted of 45 species (Table 7.1) planted as part of a restoration project in Doi Suthep-Pui National Park in northern Thailand in 1998, 1999 and 2001. Species planted only in 2000 were not used here due to unusual growth in that plot (see Chapter 5).

Table 7.1: The 45 species of tree and corresponding species code found in Doi Suthep-Pui National Park from which wood trait data and leaf trait data has been collected and which had been planted in the as part of a restoration trial in 1998, 1999 or 2000.

Species_Name	Code	Species_Name	Code	Species_Name	Code
Aglaia lawii	S123	*Ficus heteropleura*	S372	*Machilus bombycina*	S163
Alseodaphne andersonii	S101	*Ficus hispida*	S380	*Manglietia garrettii*	S007
Aphanamixis polystachya	S060	*Ficus racemosa*	S365	*Markhamia stipulata*	S204
Balakata baccata	S015	*Ficus subulata*	S039	*Melia toosendan*	S005
Betula alnoides	S048	*Garcinia mckeaniana*	S128	*Michelia baillonii*	S138
Bischofia javanica	S004	*Glochidion kerrii*	S179	*Nyssa javanica*	S146
Castanopsis acuminatissima	S270	*Gmelina arborea*	S078	*Phoebe cathia*	S379
Castanopsis calathiformis	S335	*Helicia nilagirica*	S104	*Phoebe lanceolata*	S268
Cinnamomum caudatum	S207	*Heynea trijuga*	S157	*Prunus cerasoides*	S071
Cinnamomum iners	S218	*Horsfieldia amygdalina*	S119	*Pterocarpus macrocarpus*	S092
Diospyros glandulosa	S012	*Horsfieldia thorelii*	S236	*Quercus semiserrata*	S062
Erythrina subumbrans	S317	*Hovenia dulcis*	S018	*Rhus rhetsoides*	S019
Eugenia albiflora	S325	*Lithocarpus elegans*	S280	*Sapindus rarak*	S013
Ficus benjamina	S029	*Lithocarpus fenestratus*	S337	*Sarcosperma arboreum*	S105
Ficus glaberrima	S361	*Macaranga denticulata*	S009	*Spondias axillaris*	S066

Leaf and wood samples were collected during the 2011 wet season from the 1998 and 1999 plots only and were not collected from coppiced regrowth to ensure that samples were from saplings of equal age, grown in simialr conditions and were exposed to similar environmental conditions.

7.2.3. Leaf trait data collection

Measurements, key ratios and derived fields identified by literature search were calculated and included in the analysis. Phenological leafing strategy data (deciduous, evergreen or intermediate) were collated from the Chiang Mai University Herbarium and refers to leafing patterns within the Doi Suthep-Pui National Park itself. Other sources such as the Flora of China (Zhengyi, Raven & Deyuan 1994+) and Flora of Thailand (Flora of Thailand Editorial Board 1970+) often suggest different strategies to those displayed within Doi Suthep-Pui National Park, suggesting that a number of species identified as either evergreen or deciduous may actually be facultative deciduous species (Table 7.2, see Chapter 3 for details)

Table 7.2: Leaf-trait measurements collected from 45 species of trees within the Doi Suthep-Pui National Park in Northern Thailand that have been planted as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

Descriptive variables (values)	Continuous variables (units)	Derived continuous variables (Calculation;Units)
Phenological leafing strategy (Evergreen, Intermediate, Deciduous)	Area (mm^2)	Specific Leaf Area (SLA) (Leaf Area/Leaf Dry Mass; $mm^2\ g^{-1}$)
	Wet Mass (g)	
	Dry Mass (g)	Leaf Density (Dry Mass/area*thickness; $g\ mm^3$)
	Blade Length (mm)	
	Blade Width (mm)	
	Petiole length (mm)	Petiole_Ratio (Petiole length/Blade length; ratio)
Glabrescence (Glabrous, Glabrescent, Hairy)	Leaf Thickness (µm)	
	Cuticle thickness (µm)	Blade_Ratio (Blade width/Blade length; ratio)
	N_{mass} ($mg\ g^{-1}$); N_{area} ($mg\ mm^{-2}$)	
	C_{mass} ($mg\ g^{-1}$); C_{area} ($mg\ mm^{-2}$)	DryWetRatio (Dry weight/Wet weight; ratio)
	P_{mass} ($mg\ g^{-1}$); P_{area} ($mg\ mm^{-2}$)	
Leaf Type (Simple, Compound)	K_{mass} ($mg\ g^{-1}$); K_{area} ($mg\ mm^{-2}$)	Nitrogen to carbon ratio (N:C Ratio) ($N_{mass}/C_{mass;}$ ratio)
	Na_{mass} ($mg\ g^{-1}$); Na_{area} ($mg\ mm^{-2}$)	
	Ca_{mass} ($mg\ g^{-1}$); Ca_{area} ($mg\ mm^{-2}$)	P:N Ratio (P_{mass}/N_{mass}; ratio)
	Mg_{mass} ($mg\ g^{-1}$); Mg_{area} ($mg\ mm^{-2}$)	
Leaf Margin (Entire, Partially-Toothed, Full Toothed)	Fe_{mass} ($mg\ g^{-1}$); Fe_{area} ($mg\ mm^{-2}$)	Stomatal cross-sectional area ((Stomatal Diameter/2)^2*pi; mm^2)
	Mn_{mass} ($mg\ g^{-1}$);Mn_{area} ($mg\ mm^{-2}$)	
	Stomatal Diameter (µm)	Stomatal Proportion (Stomatal Count*Stomatal cross-sectional area; proportion)
	Stomatal Count (mm^{-2})	
	Leaf breaking point (LBP) (g)	Leaf Tensile strength (LTS) (LBP /leaf thickness;$g\ mm^{-1}$
		Leaf Strength per Unit Mass (SPUM) (LBP*SLA; $g\ g^{-1}$)

7.2.4. Leaf Tensile Strength

The tensile strength of leaves was measured using a method adapted from (Balsamo *et al.* 2004). Three measurements were taken; Leaf breaking point (LBP) – (the weight that 5mm thick piece of leaf lamina could support before breaking), Leaf tensile strength (LTS, LBP/leaf thickness) and strength per unit mass (SPUM , LBP*SLA), (Table 7.3, See chapter 3 for full details).

7.2.5. Measurement of Sapling Growth

Growth data were abstracted from the FORRU database (FORRU, 2011). Three key growth measurements were made in the field; (1) root collar diameter (measured with digital calipers), canopy width at widest point and (3) height from ground level to the terminal bud (both measured using a tape measure), which were taken seventeen months after planting (after the second growing season). As only approximately 30 species were planted in each year, growth measurements from multiple years was combined to maximise species numbers. Data were abstracted for saplings planted in 1998, 1999, 2000 and 2001. The growth of species planted in more than one year was compared. Data from saplings planted in 2000 were found to be significantly different to that in other years (see chapter 5) and therefore excluded. Growth in the 1999 plot was found to be consistently 1.4 times that in the 1998 and 2001 plots. This was hypothesised to be due to a longer growing season (see chapter 5). Growth records from the 1999 plots were therefore divided by 1.4 before being combined with those from the 1998 and 2001 plots to obtain a combined score for each species. As no differences in crown width and root collar diameter were found between plots, scores were combined between years for these measurements without adjustment (see chapter 5 for details).

Table 7.3: Measures of growth for species of tree found in Doi Suthep-Pui National Park and included in germination and growth trials by the Forest Restoration Research Unit.

Measurement	Units	Calculation
Height	cm	Height at 17 months after planting
Canopy width	cm	Canopy width at 17 months after planting
Root Collar Diameter (RCD)	mm	Root Collar diameter at 17 months after planting

7.2.6. Wood Trait Data collection

Wood cores were taken from trees at breast height (1.3m) using a 5.1 mm increment borer, placed immediately into plastic bags with damp tissue and processed within 24 hours. Due to the varying diameter of trees, heartwood was available only for some of the samples. All cores were trimmed to remove heartwood to remove this inconsistency. Bark and the ends levelled to create cylinders. The length of each cylinder was measured using an electronic gauge and weighed before being dried for 3 days at 70 ◦C and re-weighed. Transverse sections of approximately 20µm thickness (thicker sections of up to 30µm thick were taken in fragile specimens) were cut from wood cores with a slide microtome. These were then step-dehydrated in ethanol and stained with 1% Safranin and 1% Alcian Blue before mounting in Euparal. Sections were observed using ImageJ software to measure the diameter of a minimum of 20 xylem vessels for each species. These measurements were then averaged to provide xylem vessel diameter and cross sectional measurements. Xylem vessel counts were made on at least five transverse sections per species and were then averaged to provide counts of xylem per mm^2. Xylem proportion was calculated as the area of a transverse wood section that consisted of xylem vessels (Table 7.4).

Table 7.4: Wood-trait Measurements collected from 47 species of trees seedlings planted in 1998 and 1999 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

Variable	Units	Calculated
Wood wet density	g mm^{-3}	Wet weight/Volume
Wood dry density	g mm^{-3}	Dry weight/Volume
Water content	g mm^{-3}	Wet density-Dry density
Xylem diameter	µm	Mean measurement
Xylem cross section	mm^2	$(\text{Xylem diameter}/2)^2 * p/10^6$
Xylem count	Count mm^{-2}	Count
Xylem proportion	Proportion	Xylem Count*Xylem cross section
Xylem conductivity	Relative	$(\text{Xylem diameter})/2)^4$
Wood conductivity	Relative	Xylem conductivity*Xylem Count
Xylem wall thickness	µm	Mean measurement
Fibre wall thickness	µm	Mean measurement
Total wall thickness	µm	Mean measurement
Tissue water content	g mm^{-3}	Water content – vessel water content
Mature tree height	m	Collated from literature
Clade	Category	Assigned using APG 111 system
Phenological leafing strategy	Category	Collated from literature

7.2.7. Statistical analysis

Generalized Linear Modeling (GLM, function 'glm') within the R statistical environment (R Development Core Team, 2012) was used to derive relationships between traits and measures of growth. Key traits and redundancy between traits were identified using previous work (See Chapter 3 and Chapter 4) and exploratory factor analysis to reduce the number of traits input into the model. All traits were normalized to a scale of 0.1 to 1.1 before analysis to account for the very large scale differences. It was sometimes valuable to simplify models by reversing the scale of a trait so that it could be combined with another trait as an interactive term within the GLM. Terms reversed in this way were prefaced with "neg".

The parsimony protocol outlined by Crawley (2007) was used to simplify the model, i.e. by removing any redundant variables and producing the Minimum Adequate Model (MAM). Here a Gaussian error structure and a log-link function was used. This process started through fitting the maximal model which a selected subset of variables and their interactions. The sub-set selected for inclusion in any given analysis was based on (1) literature information, (2) an assessment of correlations between the dependent and all possible independent variables, and (3) an exploratory factor analysis. Thereafter, non-significant values and interaction terms were removed sequentially from the highest order interactions downwards. At each step the significance of deleted items was assessed using analysis of variance using Chi-square (Crawley 2007).

7.3. Results

7.3.1. Minimum adequate models using leaf traits only

Minimum adequate models were produced for all measures of growth at 17 months after planting using leaf traits only. These produced adjusted r^2 values of 0.62 (RCD), 0.36 (height) and 0.37 (canopy width), (Models not shown here). The effectiveness of models was increased by separating species into evergreen and deciduous species (models were not produced for intermediate species as the low number of cases (n=7) caused very low adjusted r^2 values), (Table 7.5). The adjusted r^2 values for these new models ranged from $r^2 = 0.50$ (deciduous height) to 0.72 (deciduous RCD).

The deciduous models consisted mainly of chemical constituents described in the Leaf Economic Spectrum (phosphorus and nitrogen). The model for deciduous species RCD contained leaf phosphorus and nitrogen concentrations (Table 7.5b). The deciduous canopy width model suggests that species with wide canopies have glabrous leaves, with high leaf sodium concentrations and low leaf iron concentrations. The deciduous height model was more complex, containing phosphorus, iron and nitrogen.

Whilst deciduous models consisted mainly of leaf traits linked to leaf chemical constituents, evergreen models were primarily composed of morphological features (Table 7.5a). Whilst individual items within models differed, they consisted of two pairs of traits that co-varied strongly; a), leaf density and thickness, which displayed a negative correlation ($p<0.001$) and b) blade width and petiole ratio, which displayed a positive correlation ($p= 0.002$). Evergreen species with thinner, denser leaves grew faster in all evergreen models, as did species with wider leaves and longer petioles. Additionally, in the height model, species with a toothed margin grew faster than those with an entire margin.

Table 7.5: Minimum adequate linear models, using leaf functional traits, for growth measures of 47 species of tree planted in 1998, 1999 and 2001 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Models for Root Collar diameter after two growing seasons (RCD), Canopy width after 2 growing seasons (Canopy Width) and height after 2 growing seasons (Height) for both evergreen (a) and deciduous (b) species. Models included all available leaf traits.

Phenological leafing strategy	Growth Measure (Adjusted r^2)	Variable	Estimate	Std. Error	t value	Pr(>|t|)	
(a) Evergreen	RCD (0.70)	(Intercept)	-5.161	3.262	-1.582	0.12727	
		Petiole_Ratio	37.657	6.178	6.095	3.23E-06	***
		Leaf_Density	21.877	7.392	2.96	0.00703	**
	Height (0.50)	(Intercept)	-29.98	23.5	-1.276	0.21525	
		Leaf_Density	165.84	43.03	3.854	0.00086	***
		Blade_Width	116.57	49.91	2.336	0.02902	*
		Leaf_Margin_BroadToothed	42.9	20.68	2.075	0.04988	*
	Canopy Width (0.57)	(Intercept)	0.34639	0.06985	4.959	5.16E-05	***
		Petiole_Ratio	0.56215	0.11955	4.702	9.78E-05	***
		Leaf_Thickness	-0.33307	0.11463	-2.906	0.00797	**
(b) Deciduous	RCD (0.72)	(Intercept)	105.33	21.17	4.974	0.00109	**
		Pmass	-153.15	38.1	-4.02	0.00384	**
		Nmass	-178.87	42.93	-4.167	0.00314	**
		Pmass:Nmass	329.65	70.37	4.684	0.00157	**
	Height (0.50)	(Intercept)	801.9	303.3	2.643	0.0384	*
		Pmass	-5163.7	1805.1	-2.861	0.0288	*
		Nmass	-1239.2	627.4	-1.975	0.0957	.
		Pmass:Nmass	3661.8	1335.8	2.741	0.0337	*
		Pmass:negFemass	2734.9	1057.9	2.585	0.0415	*
		Pmass:negNmass:Femass	3580.1	1575.9	2.272	0.0635	.
	Canopy Width (0.68)	(Intercept)	0.57008	0.14077	4.05	0.00368	**
		Namass	0.62793	0.18242	3.442	0.00879	**
		Fearea	-1.31174	0.38947	-3.368	0.00981	**
		Hairiness_Top_Hairy	-0.29307	0.09719	-3.016	0.01667	*

7.3.2. Minimum adequate models using wood traits only

Minimum adequate models using wood traits only gave r^2 values of 0.65 (Height), 0.60 (RCD) and 0.63 (Canopy width) (Table 7.6). The RCD and Canopy width models were the same, consisting of wood dry density and tissue water content (as negative contributions) and xylem conductance as a positive contribution. The height model included similar variables, with faster growing species having both high xylem vessel conductance and low wood tissue water content. However, xylem wall thickness rather than wood water content provided the negative term.

Table 7.6: Minimum adequate linear models using wood traits to predict a) Height 17 months after planting out, b) Root Collar Diameter 17 months after planting out and c) Canopy Width 17 months after planting out for 47 species of trees seedlings planted in 1998 and 1999 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU).

Growth Measure (r^2 value)	Variable	Estimate	Std. Error	t value	P	
Height (0.65)	(Intercept)	78.65	23.65	3.326	0.00184	**
	Xylem_Wall_Thickness	-79.6	34.85	-2.284	0.02749	*
	Xylem_Conductance:negTissueWaterContent	413.93	45.18	9.162	1.43E-11	***
Root Collar Diameter (0.60)	(Intercept)	44.955	6.304	7.131	1.08E-08	***
	Wood_Dry_Density	-36.198	6.985	-5.183	6.22E-06	***
	Xylem_Conductance	21.873	6.477	3.377	0.00162	**
	TissueWaterContent	-20.147	6.015	-3.35	0.00175	**
Canopy Width (0.63)	(Intercept)	184.18	23.3	7.905	8.98E-10	***
	Wood_Dry_Density	-116.12	25.81	-4.498	5.54E-05	***
	Xylem_Conductance	110.31	23.94	4.608	3.92E-05	***
	TissueWaterContent	-84.31	22.23	-3.793	0.000482	***

Separating species by phenological leafing strategy (evergreen and deciduous) improved fit for all deciduous measures, but fit for evergreen species was mostly unaffected (Table 7.5 and Table 7.6).

For evergreen species, the most significant tem in all models was the interaction term Xylem_Conductance:negTissueWaterContent. Xylem wall thickness and wood dry density were negative terms in the canopy width and root collar diameter models, whereas the height model did not contain wood dry density (Table 7.7a). All deciduous models contained wood dry density (negative) and wood conductance (positive). In the height model only, there was in addition, a negative effect on growth associated with high wood tissue water content (Table 7.7b).

Table 7.7: Minimum adequate linear models using wood traits to predict a) Height 17 months after planting out, b) Root Collar Diameter 17 months after planting out and c) Canopy Width 17 months after planting out for 47 species of trees seedlings planted in 1998 and 1999 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Species are separated into evergreen and deciduous species for the purposes of this process.

Growth Measure (r^2 value)	Variable	Estimate	Std. Error	t value	P	
(a) Evergreen						
Height (0.58)	(Intercept)	41.7	21.68	1.924	0.0669	.
	Xylem_Wall_Thickness	-72.1	34.82	-2.071	0.0498	*
	Xylem_Conductance:negTissueWaterContent	513.01	86.66	5.92	4.92E-06	***
Root Collar Diameter (0.62)	(Intercept)	20.005	8.283	2.415	0.0245	*
	Wood_Dry_Density	-18.557	9.349	-1.985	0.0598	.
	Xylem_Wall_Thickness	-13.13	7.09	-1.852	0.0775	.
	Xylem_Conductance:negTissueWaterContent	93.493	19.22	4.864	7.32E-05	***
Canopy Width (0.65)	(Intercept)	119.06	30.92	3.851	0.000867	***
	Wood_Dry_Density	-74.89	34.9	-2.146	0.043162	*
	Xylem_Wall_Thickness	-61.87	26.47	-2.338	0.028914	*
	Xylem_Conductance:negTissueWaterContent	373.51	71.75	5.206	3.20E-05	***
(b) Deciduous						
Height (0.78)	(Intercept)	238.82	68.79	3.472	0.00842	**
	Wood_Dry_Density	-231.61	75.08	-3.085	0.01501	*
	Wood_Conductance	337.92	74.34	4.545	0.00189	**
	TissueWaterContent	-132.54	81.83	-1.62	0.14397	
Root Collar Diameter (0.79)	(Intercept)	47.94	5.281	9.078	7.95E-06	***
	Wood_Dry_Density	-46.949	7.829	-5.997	0.000203	***
	Wood_Conductance	17.329	7.436	2.33	0.044726	*
Canopy Width (0.73)	(Intercept)	196.09	26.41	7.425	4.00E-05	***
	Wood_Dry_Density	-183.58	39.15	-4.689	0.00114	**
	Wood_Conductance	101.8	37.19	2.737	0.02295	*

7.3.3. Models using both leaf and wood traits

Models containing wood traits only were more effective than those containing leaf traits only. The addition of phenological leafing strategy to models increases the effect of both models using leaf traits and models using wood traits in all cases except that of height in evergreen species. Models combining leaf traits, leaf strategy and wood traits were also produced (Table 7.9) that were an improvement on models containing only wood or leaf traits in most cases (Table 7.8). However, it should be noted that they did not contain information on species with intermediate leafing strategies.

Table 7.8: Summary of adjusted r^2 values achieved for minimum adequate linear models of measures of growth for 47 species of trees seedlings planted in 1998 and 1999 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Where separate models are provided for evergreen and deciduous species, both figures are provided.

	Measure of Growth		
Traits Included in MAM	RCD	Height	Canopy Width
Wood Traits only	0.60	0.65	0.63
Wood Traits and phenological leafing strategy (evergreen and deciduous)	0.62 (E), 0.79 (D)	0. 58 (E) , 0.78 (D)	0.65 (E) , 0.73 (D)
Leaf Traits only	0.62	0.36	0.37
Leaf Traits and phenological leafing strategy (evergreen and deciduous)	0.70(E), 0.72(D)	0.50(E), 0.50(D)	0.57 (E), 0.68 (D)
Wood Traits , phenological leafing strategy and Leaf Traits	0.87 (E), 0.88 (D)	0.77 (E), 0.78 (D)	0.85 (E) , 0.84 (D)

Most combined models contained both wood and leaf traits. For evergreen species, a single interaction term consisting of high wood vessel conductance, low wood water content and thin leaves was the most significant predictor of fast growth in all models. In addition, root collar diameter increased with petiole ratio and canopy width decreased with wood dry density (Table 7.9a). For deciduous species, models were more complex; the height model consisted only of wood traits, the RCD model included P_{mass} as a negative term along with the traits (wood conductance and wood density) found in the wood trait only model (Table 7.7) and the canopy width model for evergreen species contained only wood dry density from the wood model, but replaced wood conductance with some elements of the leaf model including leaf glabrousness, sodium content and iron content (Table 7.9b).

Table 7.9: Minimum adequate linear models using both wood traits and leaf traits to predict a) Height 17 months after planting out, b) Root Collar Diameter 17 months after planting out and c) Canopy Width 17 months after planting out for 47 species of trees seedlings planted in 1998 and 1999 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Species are separated into evergreen and deciduous species for the purposes of this process.

Growth Measure (r^2 value)	Variable	Estimate	Std. Error	t value	P	
(a) Evergreen						
Height (0.77)	(Intercept)	27.55	7.93	3.475	0.00196	**
	Xylem_Conductance: negTissueWaterContent: negLeaf_Thickness	507.56	55.51	9.144	2.74E-09	***
Root Collar Diameter (0.87)	(Intercept)	0.3577	1.5264	0.234	0.81681	
	Petiole_Ratio	21.2639	4.9391	4.305	0.000263	***
	Xylem_Conductance: negTissueWaterContent: negLeaf_Thickness	79.8557	11.2592	7.092	3.17E-07	***
Canopy Width (0.85)	(Intercept)	108.85	16.03	6.789	6.34E-07	***
	Wood_Dry_Density	-85.53	21.89	-3.907	0.000708	***
	Xylem_Conductance: negTissueWaterContent: negLeaf_Thickness	372.3	39.53	9.417	2.34E-09	***
(b) Deciduous						
Height (0.78)	(Intercept)	238.82	68.79	3.472	0.00842	**
	Wood_Dry_Density	-231.61	75.08	-3.085	0.01501	*
	Wood_Conductance	337.92	74.34	4.545	0.00189	**
	TissueWaterContent	-132.54	81.83	-1.62	0.14397	
Root Collar Diameter (0.88)	(Intercept)	349.83	64.96	5.386	0.000657	***
	Wood_Dry_Density	-361.59	68	-5.317	0.000713	***
	Wood_Conductance	433.03	54.23	7.985	4.43E-05	***
	Pmass	-249.13	71.54	-3.483	0.008289	**
Canopy width (0.84)	(Intercept)	200.19	40.85	4.9	0.00271	**
	Wood_Dry_Density	-102.53	45.04	-2.276	0.06311	.
	Namass	107.24	38.6	2.778	0.03208	*
	Fearea	-281.11	75.79	-3.709	0.00998	**
	Hairiness_Category_TopGlabrous	33.59	23.37	1.437	0.20072	
	Hairiness_Category_TopHairy	-68.29	29.75	-2.295	0.0615	.

7.3.4. Predicting the growth of intermediate species

The growth of intermediate species was predicted using both the evergreen and deciduous MAMs. The results of the two models were compared to the observed measures of growth and a preferred model identified. Neither model was shown to be more effective than the other in predicting growth in intermediate species, with most species having measurements of growth predicted by a combination of both models or not predicted by either model. Due to the small number of intermediate species, it has not been possible to draw statistically significant conclusions as to traits that identify the most appropriate models for each intermediate species (Table 7.10)

Table 7.10: Comparing the accuracy of two sets of linear models (one set designed for evergreen species and the other for deciduous species) in predicting the growth of species with intermediate leaf strategies. Preferred model is selected only where at least one model can predict observed growth to within twenty percent. Alternatively, preferred model may be identified as Higher (observed measurement is higher than both predicted measurements), Lower, (observed measurement is lower than both predicted measurements), or Between (observed measurement is between both predicted measurements). Measures of growth are a) Root Collar Diameter 17 months after planting, b) Height 17 months after planting and c) Canopy width 17 months after planting for 47 species of trees seedlings planted in 1998 and 1999 within the Doi Suthep-Pui National Park in Northern Thailand as part of a restoration scheme managed by the Forest Restoration Research Unit (FORRU). Measurements are standardised to between 0.1 and 1.1

Measure of Growth	Species	Observed Standardised Mean	Predicted evergreen MAM	Predicted deciduous MAM	Preferred Model
a) RCD	*Diospyros glandulosa*	0.246	0.270	0.278	Both
	Machilus bombycina	0.374	0.193	0.446	Deciduous
	Betula alnoides	0.039	0.219	0.429	Deciduous
	Bischofia javanica	0.183	0.176	0.671	Evergreen
	Nyssa javanica	0.508	0.191	0.376	Higher
	Ficus hispida	0.531	0.287	0.339	Higher
	Alseodaphne andersonii	0.333	0.307	0.272	Both
b) Height	*Diospyros glandulosa*	0.192	0.210	0.211	Both
	Machilus bombycina	0.312	0.146	0.179	Higher
	Betula alnoides	0.315	0.180	0.451	Between
	Bischofia javanica	0.130	0.123	0.481	evergreen
	Nyssa javanica	0.312	0.118	0.241	Higher
	Ficus hispida	0.264	0.263	0.239	Both
	Alseodaphne andersonii	0.158	0.189	0.161	Both
c) Canopy Width	*Diospyros glandulosa*	0.276	0.417	0.226	Deciduous
	Machilus bombycina	0.390	0.255	0.297	Higher
	Betula alnoides	0.558	0.284	0.362	Higher
	Bischofia javanica	0.277	0.158	0.456	Between
	Nyssa javanica	0.537	0.206	0.399	Higher
	Ficus hispida	0.456	0.410	0.298	Evergreen
	Alseodaphne andersonii	0.286	0.330	0.379	Evergreen

7.4. Discussion

The growth of 45 species of tree planted in Doi Suthep-Pui National Park planted between 1998 and 2001 for which both leaf and wood trait data were available were measured after 17 months in the field and measures of canopy width, root collar diameter and height taken. A number of generalized linear models were produced from leaf and wood functional traits to assess whether functional traits could be used to predict the growth of seedlings planted in restoration projects. These models were investigated to assess the relative importance of specific traits within seasonally-dry tropical forest, and in particular, the differences between evergreen and deciduous species.

7.4.1. The role of evergreen and deciduous species

Different leaf strategies have been observed for evergreen and deciduous species in seasonally dry tropical forest with deciduous species tending towards physically weaker, but more productive leaves and evergreen species towards less productive but mechanically stronger leaves (Pringle *et al.* 2011) in line with the Leaf Economic Spectrum (Wright *et al.* 2004). Whilst phenological leafing strategy does not necessarily predict life-span (Brodribb & Holbrook 2005), deciduous species have a leaf life-span of less than one year and have a limited time each year to photosynthesise. Whilst this might suggest that deciduous species should grow more slowly than evergreen species, the opposite is found both here and elsewhere (Givnish 2002). As a drought avoidance mechanism (Levitt 1972), leaf drop during the dry season should result in a lower importance of drought tolerance features. This has been found here (see Chapter 3 and Chapter 5) and for these reasons, phenological leafing strategy was included in these models. Within the models, the predicted differing levels of importance of hydraulic-safety features between evergreen and deciduous species are supported (see below) and consideration of evergreen and deciduous species separately has assisted in the creation of better models, which describe a higher percentage of variance despite the reduction of statistical significance due to the low number of species in each phenological leafing strategy group.

7.4.2. Leaf traits as predictors of growth

The thin, wide leaves with long petioles for maximising light interception through leaf positioning found within the evergreen models are classically associated with shade tolerance (Valladares & Niinemets 2008). These shade tolerance traits are linked to faster rather than the slower growth as might be predicted due to shade tolerance being associated with short, slow growing under-canopy species. However, the traits found here are linked not to the tolerance of low light levels, but rather to the maximisation of light interception (Takenaka 1994; Niinemets 2004), and may therefore, be viewed more as shade-avoidance traits (Henry & Aarssen 1997). The opposite end of the spectrum demonstrated in evergreen species, (i.e. denser leaves with shorter petioles), may be considered a more general stress tolerance strategy, with an emphasis on reducing biomass loss through the creation of physically-strong tissue at the expense of biomass gain through maximising light interception (Grime 1977; Wright *et al.* 2004).

The deciduous models were more difficult to interpret, due to the small number of species involved. However, morphological features related to leaf strength did not feature heavily. This supports the supposition that due to their short life-span, retention of leaf biomass was less relevant (Pringle *et al.* 2011).

7.4.3. Wood traits as predictors of growth

For evergreen species, fast growth was correlated with species with both low wood water storage and high xylem vessel conductance. The fact that these variables occurred as an interaction term confirmed that fast growth occurred in species that have both of these traits simultaneously. Both traits were linked with fast rather than protective growth, and therefore, results here are in line with other findings (Muller-Landau 2004; Poorter *et al.* 2010). The negative impact of both wood density and xylem wall thickness in the models, (both traits associated with the trade-off between fast growth and hydraulic/mechanical safety) (Hacke *et al.* 2001; Sperry, Meinzer & McCulloh 2008; Wright *et al.* 2010) further supported this supposition. However, the existence of these traits independently within the model also confirms that, whilst linked, these traits do not sit on a single axis of variation

(See Chapter 4) in line with Baas *et al.* (2004). The relative importance of hydraulic traits (xylem conductance and wood tissue water content) over mechanical traits (wood dry density) supported the importance of drought stress as a factor affecting wood traits in evergreen species (Givnish 2002).

In deciduous species, wood dry density was more significant than either xylem conductance or wood tissue water content, perhaps supporting the theory of a lower importance of hydraulic features in deciduous species (Givnish 2002). The almost entire loss of wood water storage is particularly interesting as this trait has been identified as linked to drought tolerance (Borchert 1994). Wood density has been linked to growth rates through two mechanisms (Chave *et al.* 2009);

(a) A simple trade-off between the investment of available carbon in denser wood or taller trees (Enquist *et al.* 1999; Roderick 2000).

(b) A link between wood density and sap availability. As dense wood has a lower xylem proportion, less sap reaches leaves (wood conductance is lower) and therefore lower levels of photosynthesis are achieved. This in turn leads to lower biomass gain and smaller plants (Wright *et al.* 2007). The co-occurrence of wood conductance and wood density in deciduous models appeared to support this later theory.

7.4.4. Combining phenological leafing strategy, leaf traits and wood traits to predict growth

A small number of key leaf traits were included in the combined minimal adequate models. In evergreen species, a single interaction term combining high xylem vessel conductance, low wood water content and low leaf thickness again supports the concept of fast growing shade avoiders and slow growing shade tolerators. The importance of both leaf and wood traits within these models displays that, whilst there are links between leaf and wood traits, the two elements do vary independently from each other. In deciduous species, the strong emphasis on wood rather than leaf traits suggests that wood traits are more valuable predictors of growth in deciduous species than leaf traits, and perhaps also that there is a high correlation between wood and leaf traits in deciduous species.

7.4.5. Saplings with an intermediate phenological leafing strategy

Seven species were identified as having “intermediate” leaf strategies. Whilst separate linear models were created for evergreen and deciduous species, intermediate species were not modelled as a group because of the small number of intermediate species with available data and the wide range of strategies that this category covers. Intermediate species’ growth could not be predicted effectively using either evergreen or deciduous models, and further work is required.

7.4.6. Conclusions

Wood and leaf traits have been found to be valuable predictors of growth in seasonally dry tropical forest, especially when combined with phenological leafing strategy. Relationships between traits emphasise the differences between evergreen and deciduous species and the increased importance of hydraulic traits in evergreen species. More work with more deciduous species may allow more accurate relationships between leaf traits and deciduous species growth to be ascertained. The performance results found within this paper relate to seasonally-dry tropical forest in northern Thailand and it is likely that the different models found for deciduous and evergreen species are specific to such environments. It may, however, be possible to apply such models to other seasonally-dry forests, both within Asia and South America where similar environmental pressures are exerted on seedlings. It should also be noted that the growth measures used here were selected from years with similar performance. Specifically, the 2000 plots, where growth rates differed significantly were excluded from this study. Due to the extremely small number of species available for the 2000 plot, especially when separated into evergreen and deciduous species, it has not been possible to extend this approach to different years with differing weather conditions.

Whilst the specific models described within this paper may not, therefore, be universally applicable, it adds additional evidence to the efficacy of using leaf and wood traits to predict growth performance. Application of this method in similar projects where performance data is available may also be valuable.

8. Leaf, wood and seed functional traits; their relationship with each other and seedling performance in a restoration project in northern Thailand

8.1. Introduction

8.1.1. The Framework Species Approach to forest restoration

The Framework Species Approach (FSA) to forest restoration consists of a single planting of a variety of nursery-raised species to provide both shade and fleshy-fruit to attract frugivores and bring in new plant species through animal-mediated facilitation (Goosem & Tucker 1995). In order to achieve both of these aims quickly, and to promote a heterogeneous forest canopy structure, approximately 30, carefully chosen species are usually planted.

Specifically, the Framework Species Approach categorises species as defined within the succession concept and suggests planting a mixture of both pioneer species (30%) and mid-succession to climax species. The original concept of pioneer species (Swaine & Whitmore 1988) used only seed and germination traits to define species. The suggested use of pioneer and later successional species is due, not to these traits, but due to the predicted traits ascribed to pioneer and climax species by later authors (Bazzaz 1991; Whitmore 1998).

Pioneer species are planted because they are predicted to provide fast-growing cover and later-successional species because they are predicted to have larger, fleshier fruit. However, reliance on the presumed successional stage may, not identify the most appropriate species for the framework species approach;

- The predicted links between germination traits and traits desirable for the framework species approach are not universally accepted.
- The placing of species on this single axis of successional stage fails to explore other axes of variation in forest species and the strategies that may be exploited at different successional stages.
- Whilst seed germination and seedling establishment are critical stages in the life of a plant, (Silvertown *et al.* 1993; Daws *et al.* 2007; Wright *et al.* 2010) the use of nursery raised seedlings in the Framework Species Approach removes these limitations.

- Performance in natural forest (as predicted by the model) may differ from that in restoration plots for a number of reasons including;

  (a) Competition

  Competition may limit the presence of species in natural forest, but weed removal and the spacing of saplings may remove this limitation.

  (b) Environmental conditions

  Soil moisture levels, soil composition (such as organic matter content) and light intensity in degraded land may differ to that of natural forest gaps.

Selection for other desirable traits, such as early fruiting and high survival were based primarily on observation. It is possible that alternative ecological models or individual species functional traits may be better at identifying good framework species. In chapters 3, 4, 5 and 6, relationships between functional traits of leaf, seed, wood and performance traits respectively were considered within the context of;

- The worldwide leaf economic spectrum
- The worldwide wood economic spectrum
- The concepts of shade and drought tolerance characteristics
- The concept of a growth-survival trade-off

Here, the interactions between these different trait types and models were considered within the context of the pioneer/climax model and the alternative CSR model. Additionally, functional traits related to early fruiting of fleshy fruits were explored.

8.1.2. The pioneer-climax model

The pioneer concept describes the differing factors linked to survival and growth in open areas at the beginning of the succession process (Table 8.1). The original concept of pioneer species as defined by Swaine & Whitmore (1988), used only germination traits to define species (Table 8,1a &b). However, other traits linked to plant adaptations for open conditions, which experience higher levels of light intensity and drought were added by later authors (Bazzaz 1991; Whitmore 1998).

Table 8.1: Functional traits linked to pioneer and climax species (after Turner 2001) and based on traits described in Swaine & Whitmore 1988; Bazzaz (1991; Whitmore (1998)

Trait	Pioneer	Climax	Available traits or proxy	Units
(a) Fruit and Seed characteristics				
Seed size	Small	Large	Seed volume	mm^3
			Seed Dry Weight	g
Seed Number	Large	Small	Seeds per Diaspore	Count
Seed Persistence	Orthodox	Recalcitrant	Seed Storage Behaviour	Orthodox; Recalcitrant
Age first fruit	Early	Late	Age first fruit	Years
Seed Defence	Vulnerable	Well	Seed Coat Thickness	µm
		Protected	Functional Thickness	µm
Dispersal range	Large	Small		
Dispersal Type	Wind	Animal	Fruit Fleshiness	Fleshy; Thinly fleshy, Dry
			Dispersal mechanism	Wind; Animal; Other; Mixed
(b) Germination and seedling characteristics				
Germination Light Preference	Sun	shade	Shade germination Rate/ Sun germination rate	Ratio
Germination rate	Low	High	Germination rate	Percentage
Germination Type	Epigeal	Hypogeal	Germination type	Epigeal; Hypogeal
Juvenile Mortality	High	Low		
(c) Whole Plant characteristics				
Growth rate	Fast	Slow	Nursery Growth Rate	cm $month^{-1}$
			Field Growth Rate	cm $month^{-1}$
Branching	Sparse	Copious		
Range	Large	Small	Geographical range	Km^2
			Altitude Range	Metres
Plant Life-span	Short	Long		
Adult size	Small	Large	Maximum height	Metres
Plasticity	High	Low		
(d) Leaf, Root and Wood characteristics				
Leaf Size	Large	Small	Leaf Area	Mm^2
Leaf SLA	High	Low	SLA	
			Leaf Thickness	µm
Leaf life-span	Short	Long		
Leaf Robustness	Low	High	Leaf Tensile Strength	g/mm^2
Photosynthetic rate	High	Low	Nitrogen content by mass	µg g^{-1}
			Nitrogen content by area	µg cm^{-2}
			N:C Ratio	Ratio
Respiration Rate	High	Low		
Wood Density	Low	High	Wood dry density	g/mm^3
Root-Shoot Ratio	Low	High		

8.1.3. The growth-survival trade off

The growth-survival trade-off describes species as occurring along a single axis of fast growth with little emphasis on protective features to robust growth where growth is slower but where more protective features give a higher chance of survival (Kitajima 1996).

8.1.4. The CSR model

The CSR model (Grime 1977; Grime 1979) suggests that three plant strategies (competitor, stress tolerator and ruderal) may be described by the tradeoffs inherent to a) performance under ongoing stress and b) surviving and exploitation of severe disturbances (Fig. 8.1).

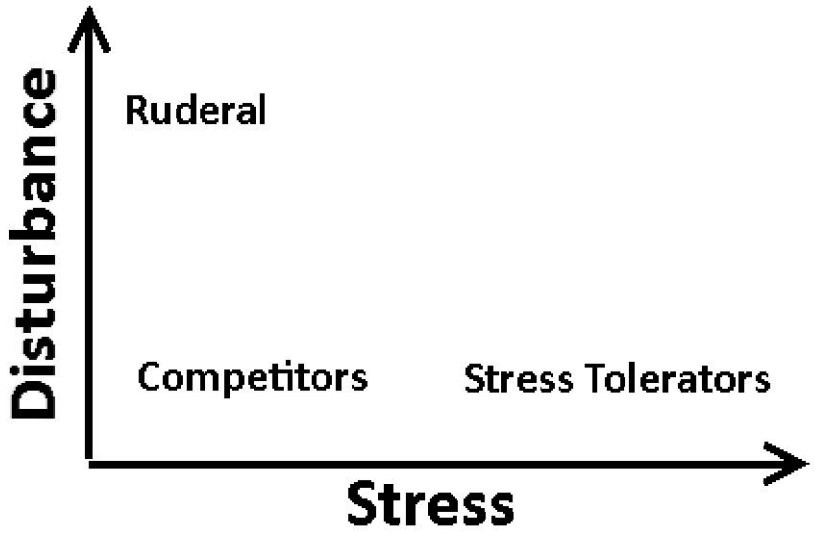


Figure 8.1: The CSR triangle model describing three plant strategies under differing levels of stress and disturbance, (Grime 1977)).

Competitor (C) – (Low stress - Low disturbance) prioritise vegetative competition for limiting resources (such as light) and use rapid growth rates, high productivity and a high capacity for phenotypic plasticity to achieve this. They achieve large size at maturity and have a life-span between that of ruderals and stress tolerator. A competitor's investment in reproduction is low relative to their vegetative expenditure (Wonkka *et al.* 2013). Competitor seeds will have high maternal investment in individual seeds. Due to their phenotypic plasticity, competitors will show large differences in growth rates between different conditions but high survival in all.

Stress-Tolerator (S) – (High stress - Low disturbance) do not compete for resources but instead, adapt to the particular limiting factor in their environment and invest heavily in resistance to damage, which results in long-lived leaves, dense wood, high rates of nutrient retention, a slow growth rate and delayed reproduction. Stress tolerating trees can get quite large (Wonkka *et al.* 2013), and have seeds with a high level of maternal investment.

*Ruderal (R). (*Low Stress – High disturbance) are fast-growing, fast reproducing opportunists that appear quickly after disturbance and rapidly complete their life-cycle whilst competition for space and resources is low at the expense of robustness (such as heavy wood or physically robust leaves) or competitive benefits (such as height). They usually attain only a small size at maturity and produce a large amount of small seeds, with thicker seed coats that are usually orthodox, remain in the seed bank and require specific triggering factors, such as light or moisture to indicate a disturbance event and break dormancy.

Maximum height and seed mass are discussed within the Leaf Height Seed (LHS) ecology strategy scheme (Westoby 1998) as representing two different aspects of the disturbance axis, in that they represent the ability of the plant to respond to disturbance at different stages of the plants' life cycle.

8.1.5. The leaf and wood economic spectra

The leaf economic spectrum (Wright *et al.* 2004), describes six traits on a single spectrum of variation (Fig. 8.2). It describes the trade-off between traits linked to emphasising biomass gain through the creation of maximum photosynthetic area at minimal cost of leaf mass, and those emphasising biomass retention through traits that increase leaf lifespan (Wright *et al.* 2004).

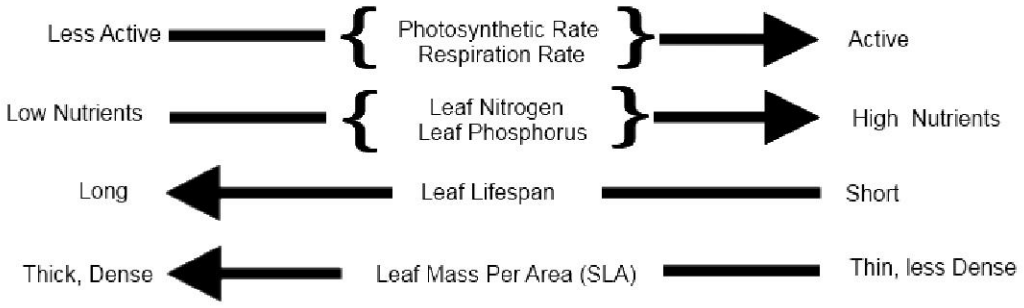


Figure 8.2: A summary of the Leaf Economic Spectrum after Wright (2004), showing the leaf traits classically associated with the prioritising of fast biomass gain to the left and the prioritising of the retention of existing biomass on the right.

The Wood Economic Spectrum is less developed than the Leaf Economic Spectrum but contains a similar axis of variation represented primarily by wood dry density, a feature linked to physical strength and protection from mechanical damage (Chave *et al.* 2009). However, the Wood Economic Spectrum also considers traits linked to hydraulic safety. The extent to which these axes co-vary has been explored but either no correlation was found (Wright *et al.* 2007), or a trade-off between these two forms of protective feature identified (Baraloto *et al.* 2010).

8.1.6. Relationships between different ecological models and concepts

A relationship between the leaf traits of the leaf economic spectrum survival/growth trade-off concept has been recorded (Sterck, Poorter & Schieving 2006), as has a link between survival and wood density, a key trait within the wood economic spectrum (Enquist *et al.* 1999). Other authors however have found that hydraulic architecture is a better predictor of growth rates than robustness in the form of wood or leaf density (Zhang & Cao 2009; Fan *et al.* 2012). Various authors have found links between wood and leaf economic spectrum traits such as SLA and wood density (Wright *et al.* 2007) but the extent t which these key traits interact with each other and plant growth in seasonally-dry tropical forest is as yet unclear.

The growth survival trade-off has obvious parallels with the leaf economic spectrum and the wood economic spectrum. It also appears to be linked to the CSR model; identifying ruderal and stress-tolerator types but without the addition of the competitor type. The competitor, with its emphasis on plasticity may be considered to possess both sets of traits. The pioneer concept combines elements of both axes of variation (stress and disturbance) within the CSR triangle and identifies a specific group of species that is similar to the ruderal species of the CSR triangle, but specifically includes functional traits linked to drought tolerance (Table 8.1).

8.1.7. Hypotheses and aims

In chapter 3, key leaf functional traits and their interactions were considered. Within chapters 4 and 6, the same was done with wood and seeds respectively. Here, an attempt is made to find relationships between key traits from all of these groups. Specifically, traits desirable for framework species, such as fast growth and early fruiting were assessed against functional traits and the results considered in terms of both the pioneer-climax model and the CSR model. The following hypotheses were tested;

- "Fast biomass gain" leaf economic spectrum traits are linked to faster seedling growth, low wood density, wider xylem vessels and small, orthodox seeds.

- Smaller seeds have less dense wood, leaves with higher SLA when orthodox and recalcitrant seeds are considered separately

- Species with higher germination in exposed conditions (Pioneer species - *sensu stricto*) have other traits linked to pioneer species i.e high SLA, low wood density and early fruiting.

- Species with orthodox seeds have high SLA and low wood density have other traits linked to pioneer species i.e high SLA, low wood density and early fruiting.

In addition, the survival and growth characteristics of species that were found in chapter 5 were considered against functional traits of these species in an attempt to identify possible reasons for these differences in performance.

8.2. Methods

8.2.1. Site

The Doi Suthep-Pui National Park (created in 1981) is an area of approximately 260 km^2 of seasonally-dry tropical forest near Chiang Mai in Northern Thailand (18.83203°N / 98.88805°E) and ranges from 340 to 1680m a.s.l (Maxwell & Elliott 2001). Whilst annual rainfall is high, rainfall in January and February can be as low as 6 mm a month, rising after the start of the monsoon in April or May to a peak of 275mm in August before dropping swiftly from October. The dry season is sub-divided into the cool-dry season (November–January) where maximum temperatures range from 30 ^{o}C to 32 ^{o}C and the hot-dry season (February– April), with a maximum daily temperature of between 30 ^{o}C and 39 ^{o}C (Fig. 8.3.).

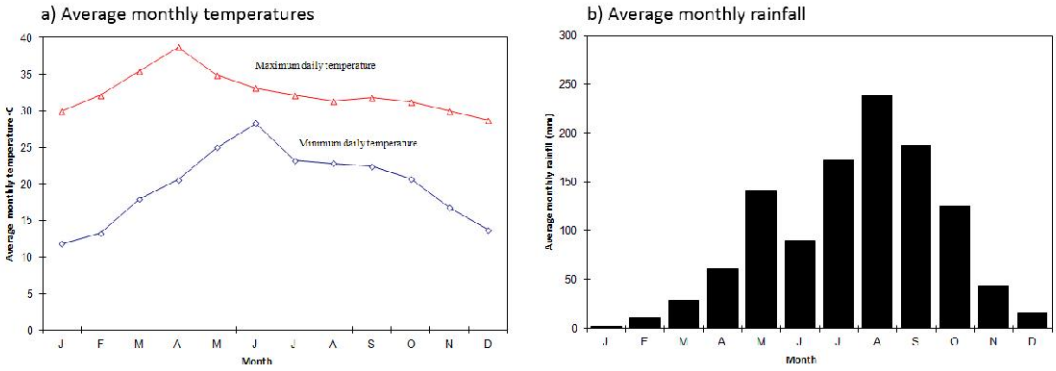


Figure 8.3: Monthly (a) maximum and minimum daily temperature and (b) rainfall in the Chiang Mai area of northern Thailand. Based on records from between 1952 and 1997– (Maxwell & Elliott 2001)

Rainfall patterns varied significantly between the years in the study. In 1998, the peak in rainfall in May was as expected but rainfall later in the wet season was slightly lower than average. In 1999 after a very rainy May, the period from June to September experienced lower rainfall than usual. In 2000 a high early peak led to a large drop in July and a reduced and delayed later rainy season. The late rainy season in 2001 was particularly wet and there was not a large drop in rainfall between the first and second peak. Both the early and late peaks of rainfall were high in 2002.

8.2.2. Functional trait data collection

Maximum tree height and phenological leafing strategy data were extracted from a variety of published and unpublished sources including the Flora of China (Zhengyi, Raven & Deyuan 1994+), Flora of Thailand (Flora of Thailand Editorial Board 1970+) and the Chiang Mai University Herbarium Database (CMU, 2011) (See Chapter 4).

Seed size and weight data as well as categorical data on seed storage behaviour, germination type and fruit fleshiness were collected from the FORRU database (FORRU, 2011) and the Royal Botanic Gardens Kew Seed Information Database (Royal Botanic Gardens Kew 2008) and augmented with samples collected from the field and from herbarium specimens (see Chapter 6).

Wood density was assessed using the method of Chave (2002). For all other wood data collection methods see chapter 4. Xylem vessel conductance and wood conductance were calculated using a simplified Hagen-Poisseuille equation from xylem diameter and xylem per mm to correct for the decreased efficiency of narrower vessels. Cavitation resistance was calculated from xylem diameter and full wall thickness (See Chapter 4).

Leaf trait, measurement and chemical data were based on field samples collected during 2011 (see Chapter 3). Leaf breaking point was measured using an adapted version of a method detailed in Balsamo *et al.* (2004). Leaf tensile strength (LTS) and leaf strength per unit mass (SPUM) were calculated (see Chapter 3).

8.2.3. Performance data collection

Germination data was extracted from the FORRU database (FORRU, 2011), the result of trials on over 400 species between 1996 and 2001 (see Chapter 6). Experimental field plots were established by FORRU in the north of Doi Suthep-Pui National Park in 1997 (Elliott *et al.* 2002; Elliott *et al.* 2003). The data presented in this paper were derived from seedlings planted in 1998, 2000 and 2001 (Table 8.2),(see Chapter 5 for details).

Table 8.2: Species of seedling planted in 1998, 1999, 2000 and 2001 as part of a restoration project on Doi Suthep-Pui National Park in Northern Thailand. Species code provided in brackets

	Planted in each year					Planted in each year			
Species	**98**	***99***	**00**	**01**	***Species***	**98**	***99***	**00**	**01**
Bischofia javanica (S004)	ü			ü	*Garcinia mckeaniana (S128)*	ü			
Melia toosendan (S005)	ü	ü		ü	*Michelia baillonii (S138)*		ü		ü
Manglietia garrettii (S007)	ü			ü	*Nyssa javanica (S146)*	ü	ü	ü	ü
Macaranga denticulata (S009)		ü	ü		*Callicarpa arborea (S156)*		ü		
Diospyros glandulosa (S012)	ü				*Heynea trijuga (S157)*	ü	ü	ü	ü
Sapindus rarak (S013)	ü	ü	ü	ü	*Machilus bombycina (S163)*		ü	ü	
Balakata baccata (S015)		ü	ü		*Glochidion kerrii (S179)*		ü		
Hovenia dulcis (S018)	ü	ü	ü	ü	*Markhamia stipulata (S204)*	ü		ü	
Rhus rhetsoides (S019)		ü	ü	ü	*Cinnamomum caudatum (S207)*		ü		ü
Ficus benjamina (S029)		ü	ü	ü	*Cinnamomum iners (S218)*	ü			
Acrocarpus fraxinifolius (S031)		ü			*Horsfieldia thorelii (S236)*	ü	ü		
Ficus subulata (S039)		ü	ü	ü	*Phoebe lanceolata (S268)*	ü			
Betula alnoides (S048)			ü	ü	*Castanopsis tribuloides (S269)*			ü	
Aphanamixis polystachya (S060)	ü				*Castanopsis acuminatissima (S270)*		ü	ü	ü
Quercus semiserrata (S062)	ü	ü	ü	ü	*Lithocarpus elegans (S280)*			ü	ü
Spondias axillaris (S066)	ü			ü	*Ficus semicordata (S315)*			ü	
Prunus cerasoides (S071)	ü	ü	ü		*Erythrina subumbrans (S317)*	ü	ü	ü	ü
Ficus altissima (S072)	ü		ü	ü	*Eugenia albiflora (S325)*	ü			ü
Gmelina arborea (S078)	ü	ü	ü		*Castanopsis calathiformis (S335)*	ü			
Morus macroura (S081)			ü		*Lithocarpus fenestratus (S337)*		ü		
Eurya acuminata (S086)	ü				*Ficus glaberrima (S361)*		ü	ü	ü
Pterocarpus macrocarpus (S092)		ü			*Ficus racemosa (S365)*		ü	ü	ü
Alseodaphne andersonii (S101)	ü				*Ficus superba (S368)*			ü	
Helicia nilagirica (S104)	ü		ü	ü	*Ficus abellii (S370)*			ü	
Sarcosperma arboreum (S105)	ü			ü	*Ficus heteropleura (S372)*		ü		
Horsfieldia amygdalina (S119)	ü	ü			*Phoebe cathia (S379)*		ü		
Aglaia lawii (S123)	ü				*Ficus hispida (S380)*		ü		

8.2.4. Performance categories

A number of categories and axes of variation related to performance in the field were identified and included within the analysis.

(a) Higher germination in exposed conditions (Pioneer species -*sensu stricto*)

Thirteen species (*Melia toosendan* - S005, *Macaranga denticulata* - S009, *Balakata baccata* - S015, *Acrocarpus fraxinifolius* - S031, *Ficus subulata* - S039, *Betula alnoides* - S048, *Gmelina arborea* - S078, *Eurya acuminata* - S086, *Michelia baillonii* - S138, *Callicarpa arborea* - S156, *Heynea trijuga* - S157, *Lithocarpus elegans* - S280, *Ficus superba* - S368), of which 3 were recalcitrant (*Michelia baillonii* - S138, *Heynea trijuga* - S157 and *Lithocarpus elegans* - S280) were identified as having far higher germination rates in partial shade than in full shade (see Chapter 6 for details). Due to the number of differences between recalcitrant and orthodox seeds identified the three recalcitrant species were not included in correlations or comparisons between groups.

(b) Species with early and late fruiting

Data available for first fruiting year are patchy. However, species for which fruiting is known to have occurred by 4 years after planting (16 species), and species for which no fruiting is known to have occurred by 5 years after planting (13 species) have been defined as early and late-fruiters respectively.

(c) Survival in the 1999 plots during the first year after planting

The 1999 plot suffered from very low survival in the first year after planting (see Chapter 5 for details). Survival in the 1999 plots has been included here for assessment against functional traits.

(d) Growth in the 2000 plots

Whilst growth in the 1998, 1999 and 2001 plots was similar or varied in a predicable manner and has been described in Chapter 7, growth in the 2000 plot differed significantly, with some species showing faster or slower growth in the second season after planting than might be predicted (See Chapter 5 for details). The difference between growth in the 2000 plot and that predicted from other plots has been included here for assessment against functional traits.

8.2.5. Statistical analysis

Correlations between continuous traits were performed using a Spearman rank correlation coefficient because the data were not normally distributed (highly skewed and presence of some outliers for most traits).

Where assessments were made of whether three or more samples differed significantly, the non-parametric method (Kruskal-Wallis one-way analysis method) was used, because of the highly-skewed nature of most of the continuous trait data used. Where two samples were compared, the Mann-Whitney U-test was used.

Binomial logistic regression, a form of Generalised Linear Modelling (function 'glm', family binomial) within the R statistical environment (R Development Core Team, 2012) was used to derive relationships between continuous and categorical traits, and specifically, to identify redundancy in explanatory traits through the reduction in comparison AIC statistic and the use of an anova function (χ^2 test) when comparing different models (Crawley 2007). All traits were normalized to a scale of 0.1 to 1.1 before analysis to account for the very large scale differences.

Generalized Linear Modeling (GLM, function 'glm') within the R statistical environment (R Development Core Team, 2012) was used to derive relationships between traits and measures of growth. Key traits and redundancy between traits were identified using previous work (See Chapter 3 and Chapter 4) and exploratory factor analysis to reduce the number of traits input into the model. All traits were normalized to a scale of 0.1 to 1.1 before analysis to account for the very large scale differences. It was sometimes valuable to simplify models by reversing the scale of a trait so that it could be combined with another trait as an interactive term within the GLM. Terms reversed in this way were prefaced with "neg".

The parsimony protocol outlined by Crawley (2007) was used to simplify the model, i.e. by removing any redundant variables and producing the Minimum Adequate Model (MAM). Here a Gaussian error structure and a log-link function was used. This process started through fitting the maximal model with a selected subset of variables and their interactions. The sub-set selected for inclusion in any given analysis was based on (1) literature information, (2) an assessment of correlations between the dependent and all possible independent variables, and (3) an exploratory factor analysis. Thereafter, non-significant values and interaction terms were removed sequentially from the highest order interactions downwards. At each step the significance of deleted items was assessed using analysis of variance using the χ^2 statistic (Crawley 2007).

Principal component analysis (function "prcomp") was used within the R statistical environment (R Development Core Team, 2012) to derive a small number of principal components from large multi-trait datasets. All traits were normalized to a scale of 0.1 to 1.1 before analysis to account for the very large scale differences between traits.

8.3. Results

Key leaf, wood and seed traits were related to each other and phenological leafing strategy to assess their level of correlation. Secondly, performance traits from chapters 5 and 6 were considered in relation to leaf, seed and wood traits.

8.3.1. Principal components analysis – wood and leaf traits

Leaf economic spectrum traits were identified as N_{mass}, N:C Ratio, SLA and LBP (see Chapter 3). All traits were standardised to between 0 and 1, and a principle component analysis was undertaken.

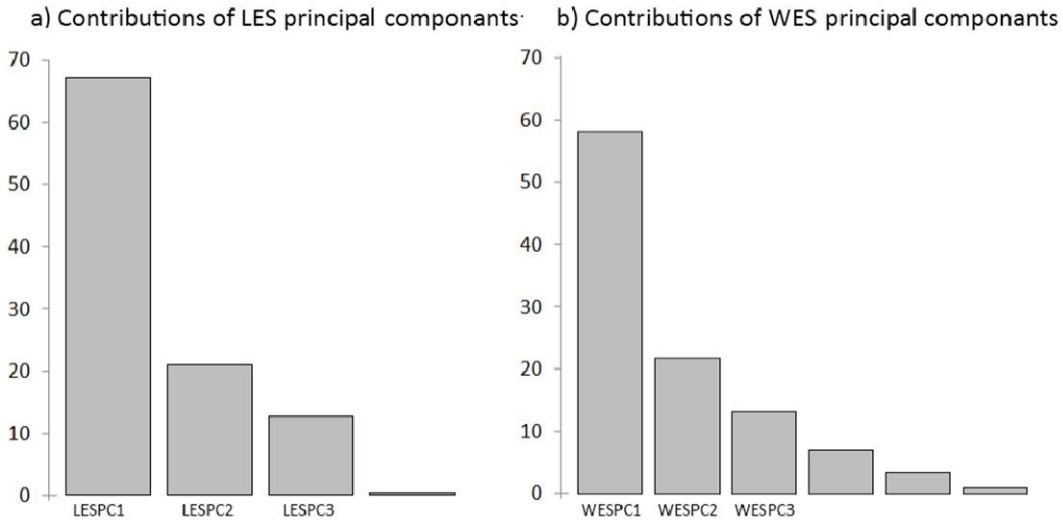


Figure 8.4: Scree plots of principal components of the a) Leaf economic spectrum and b) Wood economic spectrum for 53 species of tree found in the seasonally dry forests of northern Thailand.

Table 8.3: Variable loadings of principal components of the a) Leaf economic spectrum and b) Wood economic spectrum for 53 species of tree found in the seasonally dry forests of northern Thailand.

a) Leaf economic spectrum					b) Wood economic spectrum						
	PC1	PC2	PC3	PC4		PC1	PC2	PC3	PC4	PC5	PC6
NC Ratio	0.51	-0.43	0.22	0.71	Wood Dry Density	0.22	0.21	-0.93	-0.16	0.17	0.08
Nmass	0.51	-0.40	0.29	-0.70	Xylem diameter	-0.63	0.03	-0.19	0.17	0.18	-0.71
SLA	0.50	0.09	-0.86	-0.04	Tissue water content	-0.17	-0.90	-0.27	-0.14	-0.24	0.09
LBP	-0.47	-0.81	-0.36	-0.04	Vessel conductance	-0.56	0.06	0.06	-0.36	0.51	0.54
					Wood conductance	-0.33	0.36	-0.07	-0.45	-0.75	0.03
					Cavitation Resistance	0.31	-0.09	0.16	-0.78	0.25	-0.44

The first Leaf economic spectrum principal component (LESPC 1), described 67% of the variation within traits of the leaf economic spectrum (Fig. 8.4a) and consisted of positive contributions from SLA, N:C Ratio and N_{mass} and a negative contribution from leaf breaking point with approximately equal contributions of all traits. It therefore suggested a single axis of variation in the leaf economic spectrum. In deciduous species LESPC1 was also correlated with leaf Sodium concentation ($p=0.0004$). LESPC2, accounting for 20% of the variation, was largely contributed to by differences in LBP, but also, to a slightly lesser degree by N:C Ratio and N_{mass}. LESPC2 showed a very high negative correlation with SPUM (Leaf strength per unit mass), ($p<0.001$), indicating that this axis represented the efficiency of strengthening tissue within a leaf. LESPC3, accounting for 12% of variation in leaf economic spectrum traits was closely correlated with N_{area} ($p<0.001$) and therefore appears to represent the photosynthetic efficiency of an area of leaf tissue. In evergreen species LESPC3 was correlated with petiole ratio ($p<0.001$) and blade ratio ($p= 0.003$).

A second principle component analysis of wood traits was undertaken using wood dry density, Xylem vessel diameter, water content of wood tissue, Xylem vessel conductance and wood conductance. The first wood economic spectrum principal component (WESPC1), explained 58% of variation and was correlated negatively with xylem diameter, and positively with cavitation resistance ($p<0.001$ in both cases), and therefore, appeared to represent variation from water transport efficiency to water transport safety. WESPC1 was also correlated with wood dry density ($p=0.001$). WESPC2 (contributing 18%) was correlated negatively ($p<0.001$) with water content held in wood tissue. WESPC3 (contributing 14%) was correlated negatively with wood dry density ($p<0.001$). These three principal components therefore appear to represent hydraulic capacity, water storage capacity and wood mechanical strength respectively.

8.3.2. Leaf and wood trait correlations

In evergreen species, none of the LES principal components were correlated with wood traits, or any of the WES principal components. However, when all leaf traits were considered, WESPC2 was correlated negatively with Ca_{mass} (p=0.002), and positively with leaf area (p=0.005) and cuticle thickness (p=0.008). WPC3 and wood dry density were correlated positively with petiole ratio (p=0.002 and p=0.001 respectively) and negatively with Leaf tensile strength (p=0.001).

In deciduous species, there were positive correlations between LESPC1 and traits linked to efficient water transport in wood such as wider xylem (p=0.003) and xylem vessel conductivity (p=0.002) as well as a negative correlation with WESPC1 (p=0.002). When individual LES components were considered, these relationships were the same. However, SLA was negatively associated with wood conductance.

WESPC1 was correlated negatively with N:C Ratio (p= 0,003), Nitrogen concentration (p=0,004) and to a less significant degree with SLA (p= 0.048). WESPC1 was uncorrelated to leaf breaking point (LBP). WESPC1 was also correlated with blade length (p=0.001). Other key correlations included correlations of wood water content and Blade ratio (p<0.001 as well as between wood dry density and leaf density (p=0.006).

8.3.3. Wood and leaf traits linked to seed traits

Orthodox seeds were smaller than recalcitrant seeds, had more seeds on average per diaspore and have a lower Shade:Sun Germination rate (see Chapter 6 for details). Orthodox species had leaves at the fast-biomass gain end of the leaf economic spectrum and low density wood. Due to these key differences between orthodox and recalcitrant species, the two groups were considered separately when considering their relationships to wood and leaf traits. In orthodox seeds, seed size was correlated negatively with wood tissue water content (p= 0.001) and positively with maximum height (p= 0.002). Larger seeds also had weaker leaves (lower LBP) (p= 0.001) with lower Calcium concentrations (p=0.006) but no relationships with other members of the leaf or wood economic spectrum were

observed. In recalcitrant species only, species with larger seeds had bigger leaves ($p<0.001$) with longer petioles ($p=0.003$), but no relationships with leaf or wood economic spectra traits were found.

8.3.4. Traits linked to growth rates in the field

Growth in the second season after planting in the 1998, 1999 and 2001 plots was correlated positively with LESPC1 ($p=0.009$) and WESPC3 ($p=0.006$) , but negatively with WESPC1 ($P<0.001$). When individual traits within the leaf economic spectrum were considered, growth rates were correlated (negatively) only with leaf breaking point ($p=0.002$) and not with SLA, N_{mass} or N:C Ratio. Growth was however, also, correlated negatively with leaf thickness ($p=0.006$) and strength per unit thickness ($p=0.002$). When individual traits within the wood economic spectrum were considered, growth was negatively correlated with wood dry density ($p<0.001$) and wood water tissue content ($p=0.006$), but unrelated to any hydraulic traits.

8.3.5. Identification of pioneer species *(Sensu lato)*

Species with both higher than average SLA and lower than average wood dry density were identified as fitting the description of pioneer species. These ten species (*Melia toosendan* - S005, *Manglietia garrettii* - S007, *Macaranga denticulata* - S009, *Hovenia dulcis* - S018, *Spondias axillaris* - S066, *Gmelina arborea* - S078, *Nyssa javanica* - S146, *Erythrina subumbrans* - S317, *Ficus superba* - S368 and *Ficus hispida* - S380) were considered to see whether they possessed other traits linked to the pioneer concept. They all had small orthodox seeds, and had higher germination rates in partial shade than full shade ($p=0.036$) (See section 8.3.6). They also had longer petioles ($p=0.012$), more rounded leaves ($p=0.016$), faster growth in the nursery ($p=0.040$) and faster growth the field ($p=0.001$). Their maximum height was no shorter than other species, ranging from 10m to 40m. However, all of these traits are also linked to possession of orthodox seeds, and when the ten species were compared only to other orthodox-seeded species, no significant differences were found.

8.3.6. Light preferred for germination

Shade-over-sun germination rate was correlated with a number of functional traits traditionally associated with pioneer species when all species were considered as a whole. However, shade-over-sun germination was strongly linked to seed storage behaviour and, when recalcitrant and orthodox species were considered separately, no such correlations were found. Shade-over-sun germination rates were correlated negatively with growth rate over the second season in the field ($p=0.006$). Species that had germination rates in partial shade over twice that in full shade were classified as light-preferring. These thirteen species (see 8.2.4) were mainly orthodox and epigeal, with three recalcitrant, the ten orthodox species were compared to other orthodox seeds and to recalcitrant species with no preference for sun germination. Light-preferring seeds were generally orthodox, small (smaller even than other orthodox species), and with epigeal germination (see Chapter 6). Functional seed coat thickness was greater in light-preferring species than other orthodox species and similar to recalcitrant species.

Along with other orthodox species, light-preferring species had higher N_{mass}, and N:C Ratio than recalcitrant species (Students T test, $p=0.002$ and $p<0.001$ respectively), (Fig. 8.5a) and a lower leaf breaking point, but no difference was found between light-preferring and non light-preferring orthodox species (Fig. 8.5b). Light-preferring species had higher first year survival in 2001 but other than this single example could not be separated by performance from other orthodox species. The maximum height of light-preferring species was smaller than other groups, including other orthodox species. (Students T test, $p=0.042$, Fig. 8.5c), but they did not have smaller leaves than other species, or differ in terms of SLA or leaf thickness. Wood dry density was greater in recalcitrant species than either orthodox group (8.5d).

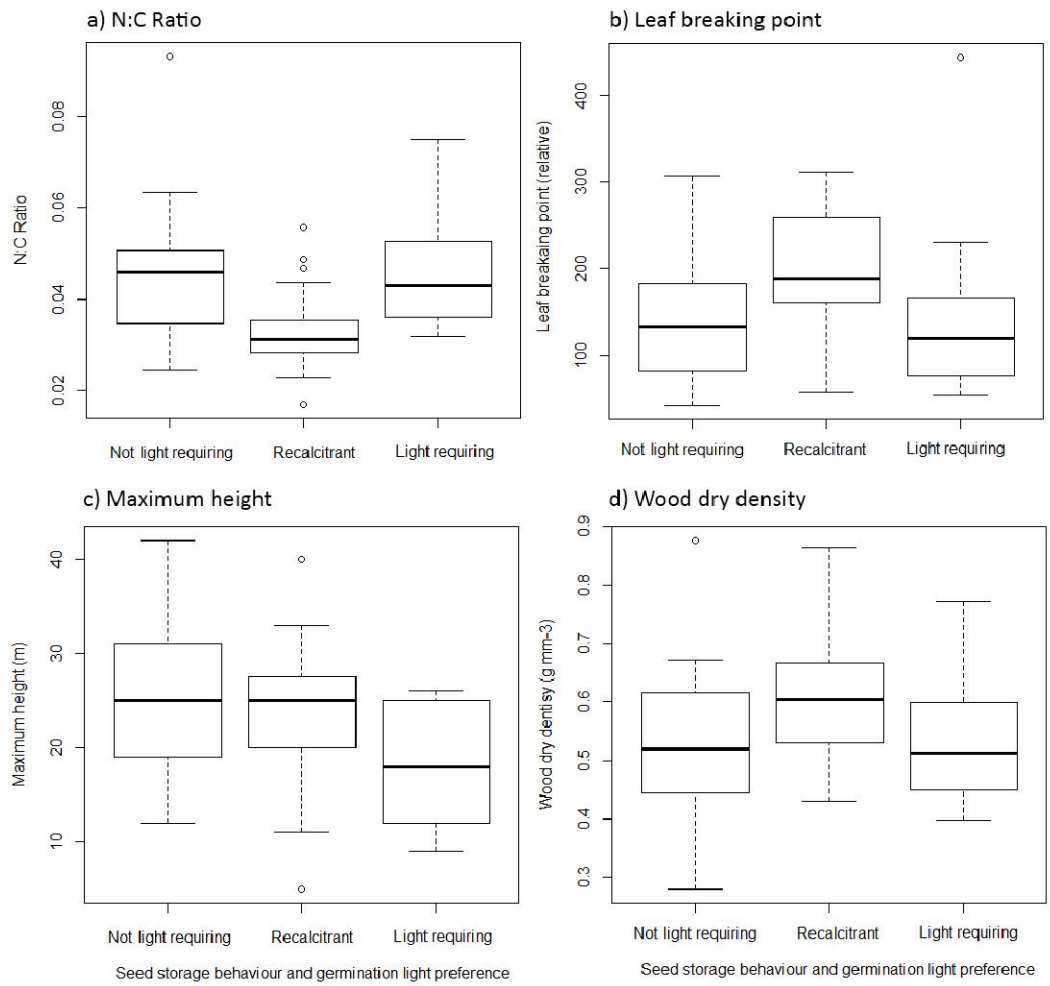


Figure 8.5: Functional traits of species with orthodox seeds that do not germinate more effectively in full sun than partial shade, orthodox species that do germinate more effectively in full sun and partial shade and species with recalcitrant seeds for 53 species found in the seasonally-dry tropical forest of northern Thailand.

8.3.7. Predicting age at first fruiting

Age at first fruiting was not available for all species and in some cases was available only in crude form i.e. not by 6 years. Therefore, data were condensed into categories, early fruiters (fruiting by 4 years after planting), late fruiters (no fruit by at least 5 years after planting) and unknown. Fifteen early fruiting and 16 late-fruiting species were identified. The maximum height for early fruiters was significantly smaller (Students T test, p=0.008), than for late fruiters (Fig. 8.6). By considering evergreen and deciduous species separately, two distinct groups of early fruiting tree were identified, with early fruiting evergreens being very short, but early-fruiting deciduous species being mid-range, similar to the height of evergreen late fruiters. Deciduous late fruiters tended to be very tall.

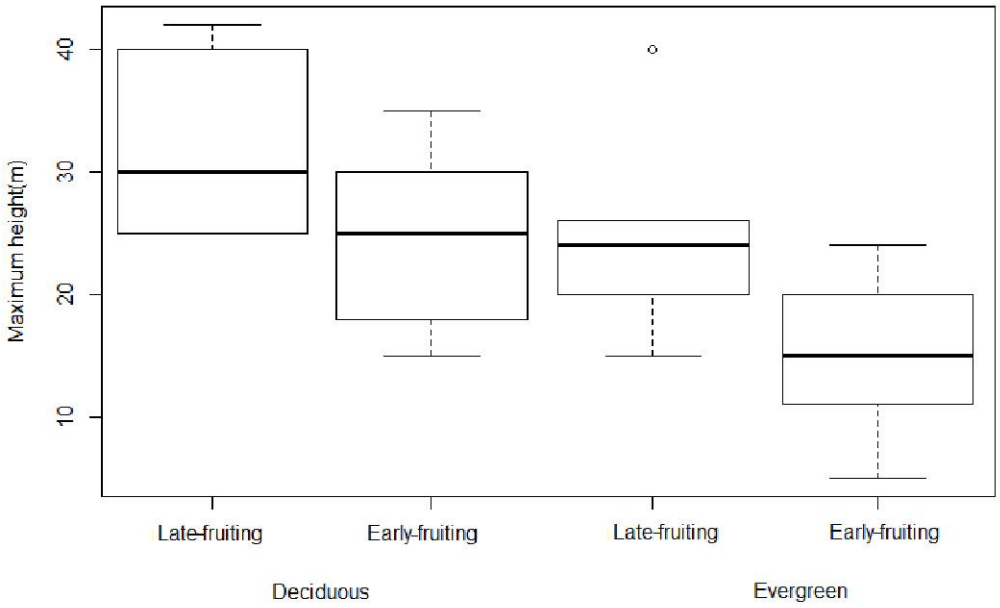


Figure 8.6: Maximum height for early and late fruiting species of tree found in the seasonally dry tropical forest of northern Thailand. Species are divided into evergreen and deciduous species.

No significant links were found between fruit fleshiness and early or late fruiting, However, 5 species of early fruiting deciduous species did have somewhat fleshy fruits.

Table 8.4:Cross tabulation of fruit fleshiness and distributor with early and late fruiting for 54 species found in the seasonally-dry tropical forest of northern Thailand.

	Fruit fleshiness and seed distributor			
Early or late fruiting and phenological leafing strategy	Fleshy	Somewhat fleshy	Dry fruit: Wind distributed	Dry fruit: Animal distributed
Early deciduous	0	5	1	0
Early evergreen	2	3	0	1
Early intermediate	2	1	0	0
Late deciduous	1	3	2	0
Late evergreen	1	2	0	3
Late intermediate	2	1	1	0
Unknown deciduous	3	0	1	0
Unknown evergreen	7	5	0	4
Unknown intermediate	2	0	0	0

Deciduous early-fruiters had fast growth in the nursery and physically weak leaves. Although they had small seeds in comparison to late-fruiting evergreens, they had seeds of similar size to other deciduous species. The functional seed coats of these species were thicker than other deciduous species. Evergreen early-fruiters however had very slow nursery growth, leaves of average strength and very small seeds with very thin seed coats (Fig. 8.7).

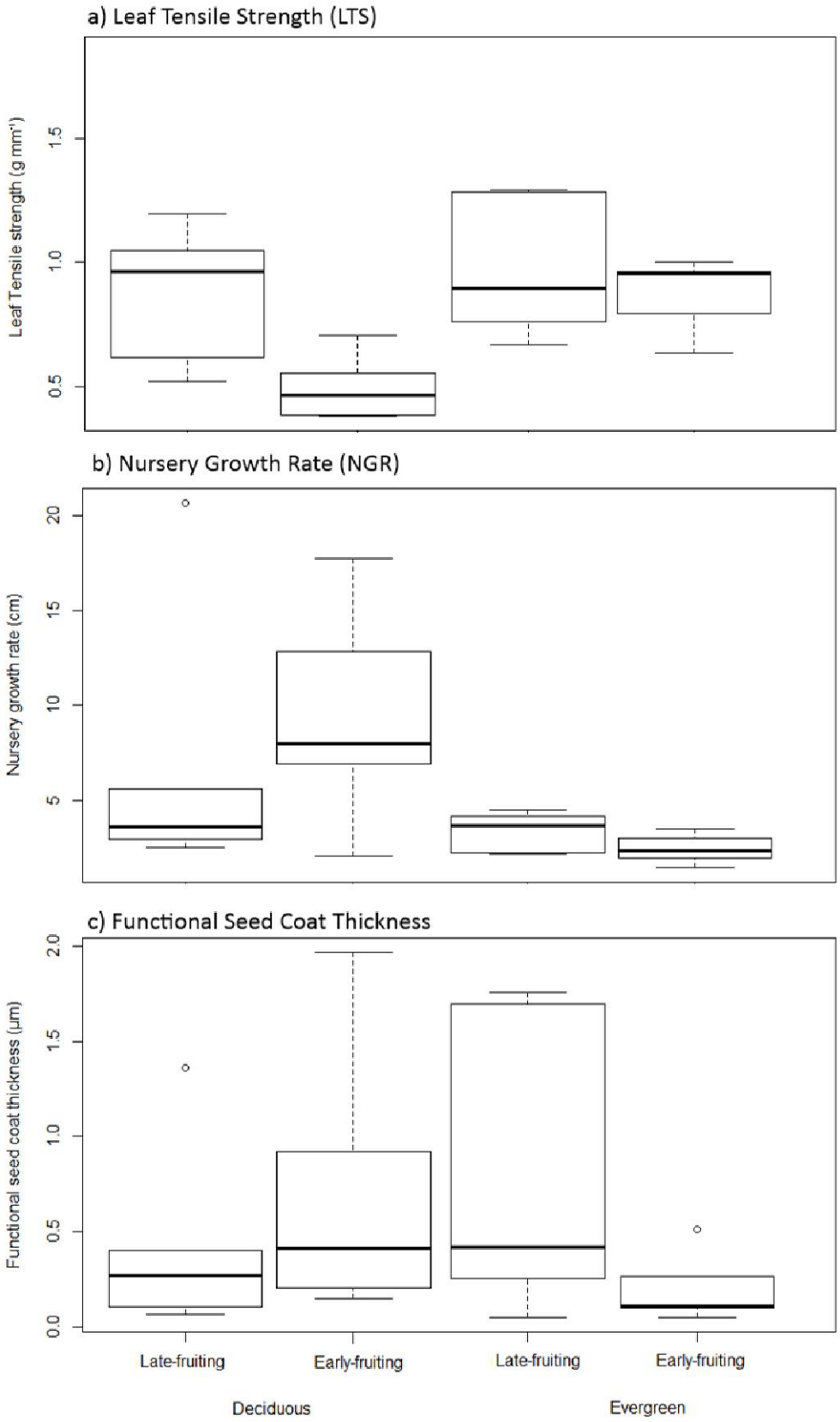


Figure 8.7: a) Leaf Tensile Strength, b) Nursery growth rate and c) Functional Seed Coat Thickness of early and low fruiting species with deciduous and evergreen leaves for 53 species of tree found in the seasonally-dry tropical forest of northern Thailand.

8.3.8. Survival in the 1999 plots during the first season after planting

Survival in the 1999 plots was negatively correlated with seed volume (p=0.001) and wood density (p=0.001) and positively correlated with Ca_{mass} (p<0.001). The six species with high (greater than 80%) survival (*Hovenia dulcis* -S018, *Rhus rhetsoides* - S019, *Ficus benjamina* - S029, *Ficus glaberrima* - S361, *Ficus racemosa* - S365 and *Ficus hispida* - S380) had orthodox seeds that did not show a preference for germination in full sunlight compared to shade. Of these six species, four were ficus and the other two had small, single-seeded bird-dispersed fruits. The five low (less than 40%) surviving species (Sapindus rarak - S013, Acrocarpus fraxinifolius - S031, Horsfieldia thorelii - S236, Lithocarpus fenestratus - S337, Phoebe cathia - S379) showed no pattern based on phenology, seed storage behaviour or germination but all had short petioles as a proportion of their leaf blade length.

Comparison of survival groups indicated that, whilst wood density was correlated negatively with survival, the highest and lowest survival groups were not in the highest and lowest wood density groups. In fact, the six species with highest wood density (*Glochidion kerrii* - S179, *Castanopsis acuminatissima* - S270, *Callicarpa arborea* - S156, *Horsfieldia amygdalina* - S119, *Quercus semiserrata* - S062, *Pterocarpus macrocarpus* - S092) and the three species with the lowest wood density (*Erythrina subumbrans* - S317, *Gmelina arborea* - S078, *Balakata baccata* - S015) had middle level survival .

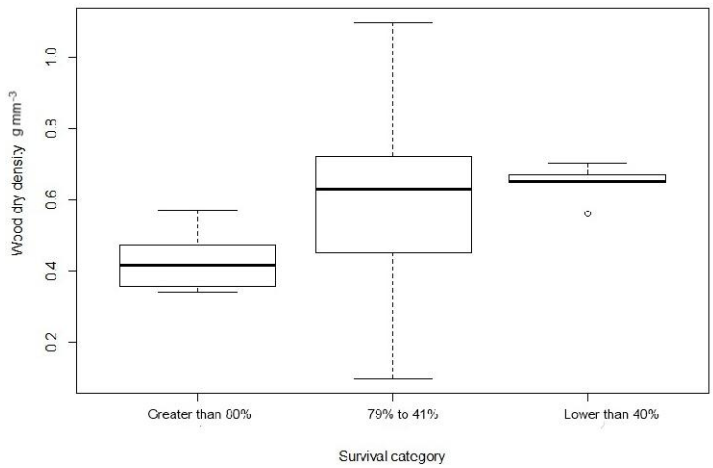


Figure 8.8: Differing wood densities in species of tree identified as high, medium and low surviving during the first season after planting in 1999 as part of a forest restoration project by the Forest Research Restoration Unit (FORRU) in Doi Suthep=Pui National Park in northern Thailand

8.3.9 Growth in the 2000 plots during the second season after planting

Growth in the 2000 plots over the second year after planting (during 2001) was more variable than in other plots, (see Chapter 5 for details). Species with fast growth in 1998, 1999 and 2001 grew slower than expected in the 2000 plot whereas approximately half of those species that grew slowly in other years had faster, and about half slower in the 2000 plot (Fig. 8.9).

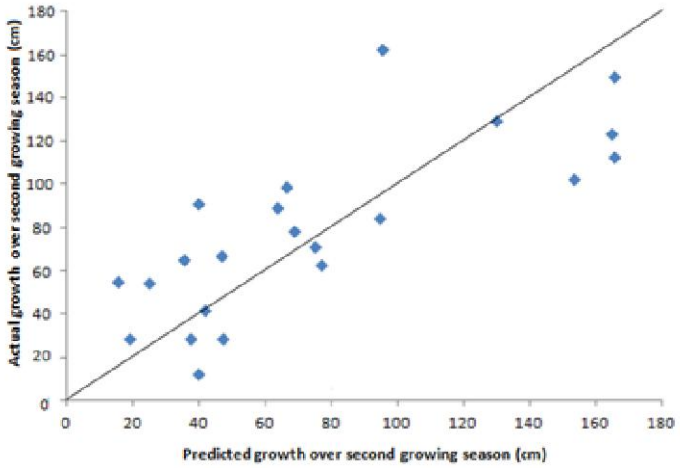


Figure 8.9: Growth during the second season after planting in the 2000 plots for species of tree planted as part of restoration project in Doi Suthep-Pui National Park in northern Thailand compared to that which would be predicted based on performance in other years.

Growth in the 2000 plots as a ratio of growth in other years was assessed against other variables. Initial correlations confirmed a negative correlation with growth rates in other years (p=0.004), but also suggested the role of calcium and leaf strength per unit mass in the relationship (p=0.03 and p=0.02 respectively). Growth rates in the 1998, 1999 and 2001 plots provided an adjusted r^2 value of 0.41 when used alone to predict growth rates in the 2000 plots. The addition of Ca_{mass}: SPUM, improved the fit to an adjusted r^2 value of 0.69. Fast growth in other plots provided a negative effect on growth achieved in 2000. (Table 8.5)

Table 8.5: Minimum adequate linear models for the ratio of growth in the second season after planting in the 2000 plots against the predicted growth based on performance in other plots.

Variable	Estimate	Std. Error	t value	P	
(Intercept)	0.38353	0.08794	4.361	0.000336	***
H23_otherplots	-0.3394	0.10674	-3.18	0.004934	**
Ca_{mass}:SPUM	0.67964	0.15752	4.315	0.000374	***

8.4. Discussion

Key traits such as SLA, wood density and seed size were compared and relationships interpreted in line with the pioneer concept and the CSR model.

Traits desirable for restoration planting schemes such as germination rate, growth rate, survival in the field and time of first fruiting were considered in detail to see whether they could be predicted from available traits and whether the CSR model (and its component elements) might be a better model for selecting species with desirable traits for restoration purposes.

8.4.1. The CSR model

In deciduous species, the strong correlations between "fast growth" leaf traits and hydraulically efficient wood traits supports the assertion that more actively photosynthesising leaves require more water. It also supports the assertion that it is hydraulic wood traits rather than mechanical wood traits that relate wood features to both the Leaf Economic Spectrum and to seedling growth rates (Muller-Landau 2004; Poorter 2008; Wright *et al.* 2010). It differs from a number of local studies that found that leaf and stem traits vary independently (Wright *et al.* 2007; Baraloto *et al.* 2010). However, the focus of these correlations (hydraulic safety) may explain this discrepancy.

The lack of such relationships found here in evergreen species is probably due to the truncated range of both leaf and wood traits; evergreen species possess traits mostly at the robust end of both the LES and WES, whereas deciduous species cover a broader range of values.

The correlations in evergreen species between wood dry density and both leaf tensile strength (LTS) (positive) and petiole ratio (negative) appear to demonstrate an axis of variation between shade tolerance as stress-tolerance (a strategy of physical strength and biomass loss reduction) and shade-tolerance through the maximisation of sun interception), (Henry & Aarssen 1997) .

Here, the CSR model predicted correlations between the leaf economic spectrum traits or wood economic spectrum traits and seed size were not supported.

8.4.2. The pioneer concept

Neither the narrow (species germinating better in open conditions) nor broad (see 8.3.5) definition of pioneer species contributed more to predictions of growth in the nursery or field than simply identifying species by seed storage behaviour.

The pioneer model suggests that pioneer species will have be early-fruiting. This was not supported if germination requiring sun is used as the definition of pioneer species as no significant difference in shade-over-sun germination rate was found between early and late fruiting species. However, the deciduous early-fruiters, with their fast growth, small seeds, weak leaves and short stature fit with both the broader pioneer and ruderal model concepts of fast growing species that reproduce quickly. This does not fit the original definition of pioneer species (Swaine & Whitmore 1988) but supports other findings that pioneers do not necessarily need sunlight for germination(Alvarez-Buylla & Martinez-Ramos 1992; Kyereh, Swaine & Thompson 1999). They had thicker seed coats than other orthodox species, which suggests the predicted persistence in the seed-bank (Swaine & Whitmore 1988).

The evergreen early-fruiting species do not fit this model. The slow growth of these species, despite their early fruiting, suggests an emphasis on reproduction over vegetative growth; consideration of root-shoot ratio may help in understanding this relationship.

8.4.3. Survival and growth in the field in 1999 and 2001

A trade-off is expected between shade tolerance through more “robust” leaf growth and the capacity for rapid growth in open areas (Denslow 1980; Cornelissen, Diez & Hunt 1996; Reich *et al.* 1998). Here, generally, fast growth was associated with both the leaf and wood economic spectra, with faster species having both leaves and wood at the “fast growth” rather than “robust growth” end.

However, once evergreen and deciduous species were considered separately, there were no significant correlations between growth rates over the second growing season and either wood or leaf functional traits. The relationship between growth rates and leaf and wood traits here was more fully explored in Chapter 7. However, survival in the first year after planting in the 1999 plot, and growth over the second year after planting in the 2000 plot differed significantly from that in other years and were explored here.

It was hypothesised that the low survival of species in the first season after planting in the 1999 plots was due to heavy losses soon after planting (See Chapter 5) related to establishment. A number of hypotheses were suggested, all related to the heavy rainfall in April and May as this was the most distinctive feature of the weather in that year. These included a pathogen load increase (Swinfield *et al.* 2012) exacerbated by transplantation stress and reduced effectiveness of "hardening off" (Anderson & Helms 1994), in the nursery. The best indicators of high survival during the first dry season in the 1999 plot were fast growth, (see Chapter 5), small seeds and a high leaf Ca_{mass}.

The unusual growth in the 2000 plot occurred during 2001, a particularly wet year. However, in this case, the additional rainfall fell somewhat later and affected only the period between July and November. Growth reduction or gain in the second season after planting in the 2000 plot compared to other plots was also related to growth rate and Ca_{mass}. Reduced growth was found in faster growing species and faster growth found in approximately half of the slower growing species. This faster growth was found in species with high leaf calcium levels and stronger leaves per unit mass. It would therefore appear that, whilst survival and growth rates were affected in opposite directions by maximum growth rates, high leaf calcium content was valuable in both years.

8.4.4. Potential role of Calcium

Calcium performs a number of roles within the leaf and is associated with both leaf structural support (Demarty, Morvan & Thellier 1984) and protection from heat stress through stomatal function (Macrobbie 1992). It is also associated with higher protection from a range of herbivores, including insects and mammals (Djamin & Pathak 1967; Galimuhtasib, Smith & Higgins 1992; Ward, Spiegel & Saltz 1997; Korth *et al.* 2006; Massey, Ennos & Hartley 2006; Hanley *et al.* 2007) as well as reducing the effect of fungal pathogens (Percival & Haynes 2009). As calcium does not relocate from leaves, it builds up in the leaf tissue and is therefore associated with transpiration rate and leaf age (Storey & Leigh 2004). As deciduous species are lost each year and all leaves collected here were collected over a 2 week period in a single year, a correlation between transpiration rate a Ca_{mass} should be easily identified. However, no relationship was found in deciduous species between Ca_{mass} and traits associated with transpiration (stomatal number, K_{mass}) or photosynthesis and respiration (N_{mass}, N:C Ratio) (See Chapter 3). The pathogen hypothesis therefore bears further investigation.

The relationship between seed size and survival was not linear, the correlation between seed size and survival was because whilst many small seeds had poor survival, no large seeded species had high survival. The low survival of larger seeded species may indicate a trade-off in investment between seed and leaf, as typified within the LHS model associated with the CSR triangle.

8.4.5. Predicting early fruiting

Early fruiting was found to be linked to maximum height, especially when combined with phenological leafing strategy and leaf tensile strength; early fruiters are generally evergreen species under 20m tall and deciduous species under 30m tall. Growth rate in the nursery was also found to be a useful indicator of early fruiting, but only for deciduous species. This group of early fruiting, short, deciduous species with fast growth and thin leaves fit with the description of ruderal species in the CSR triangle very well. They also fit well with the description of pioneer species. The early-fruiting evergreen species do not fit as well into any

ecological model. Early fruiting species are predicted in both the pioneer concept and the CSR triangle to have small, dry fruits with small seeds. However, neither Seed size nor fruit fleshiness were found to be a valuable indicator of early fruiting.

8.4.6. Conclusion

Neither the CSR or pioneer concept were suitable for predicting growth here. Individual traits such as wood density, hydraulic capacity or seed strorage behaviour were more useful when considered alone rather than when considered as part of a syndrome or model.

The hydraulic properties of wood were found to linked more significantly to leaf economic traits than the mechanical properties of wood, suggesting that within seasonally-dry tropical forest, an area where drought is of particular importance, these traits were more important than mechanical safety.

The importance of Calcium in predicting performance in seasonally-dry tropical forest is of interest here, possibly due to links between calcium and protection from pathogens. This theory requires further investigation.

The prediction of early fruiting using maximum height, nursery growthe rate and phenological leafing strategy is potentially very valuable, especially as data on maximum height in this case was derived from published sources rather than collected directly in the field.

9. Final discussion: conclusions, recommendations and further work

9.1. Introduction

Due to global deforestation and forest degradation (FAO 2010), there is an increasing need for large reforestation projects in many areas of the world (Lamb 2011); something recognised by a number of international conventions (www.un.org/esa/forests/about-history.html - Accessed 2013). One such method is the Framework Species Approach, which has been used successfully in both Queensland (Australia), (Goosem & Tucker 1995) and in Thailand (Elliott *et al.* 2002; Elliott *et al.* 2003). The Framework Species Approach relies on a single planting of both pioneer and later successional species to reduce limitations to succession (dispersal and initial colonization) and kick-start forest regeneration, through supplying both shade (to reduce annual and perennial weed cover that both encourages fire and stops tree seedlings from reaching adult size) and resources attractive to frugivores (to improve seed dispersal of later successional species into regenerating areas).

Seasonally-dry tropical forests, although less well studied than evergreen tropical forests (rainforests) are particularly threatened (Janzen 1988; Gerhardt 1993) and, due to their currently fragmented nature (Pennington, Lavin & Oliveira-Filho 2009) offer the opportunity to utilise reforestation methods, such as the Framework Species Approach, which rely on remnant forest (Goosem & Tucker 1995). The Forest Restoration Research Unit based at Chiang Mai University has been using the Framework Species Approach (FSA) to restore seasonally-dry tropical forest in the Doi Suthep-Pui National Park in northern Thailand and has undertaken a number of trials to identify species and methods to develop the FSA approach for regional use (Elliott *et al.* 2002; Elliott *et al.* 2003). To this end they have built a database of field performance data using a number of potential candidate species. The trials have been successful and FORRU has rehabilitated areas of the Doi Suthep-Pui National Park successfully and is now expanding its work into other areas of northern Thailand and elsewhere in south-east Asia (Laos and Cambodia). However, the trial process is expensive and labour-intensive and identifies only specific species appropriate for the forests of northern Thailand.

9.2. Project structure and aims

If performance in the field could be predicted from trait data, it would reduce the need for trials, and therefore, improve the cost-effectiveness of restoration projects. Also, by generalising the findings of the FORRU trials and linking individual species performance to broader ecological strategies and functional traits, species with similar traits could be identified in other areas, so supporting the species selection process in using this technique. It has been suggested that these trials may be targeted more effectively by pre-assessing species using easily measured physical, chemical and life-history traits (Walters & Reich 1999; Poorter & Bongers 2006).

The Framework Species Approach plants both early- and late-successional species on plots where late-successional species would not occur naturally. In this, it differs significantly from other methods such as the Accelerated Succession Approach, where successional stages are replicated with multiple plantings (Hardwick *et al.* 2004). However, the FSA also plants them as larger seedlings, which differs from direct seeding (Lamb 2011), and removes limitations due to germination, establishment or early competition with weeds.

Analysis of plant functional traits have been found useful in the classification of plant species into different functional types based on ecological strategy (Diaz & Cabido 1997; Westoby 1998; Semenova & van der Maarel 2000; Powers & Tiffin 2010) and predicting plant performance in restoration projects in other environments (Martínez-Garza *et al.* 2005). The analysis of traits linked to the specific requirements of the Framework Species Approach, considered within the context of the ecological strategies displayed by tree species in seasonally-dry tropical forest may therefore allow the identification of functional traits that predict good performance.

There is evidence that suggests that many late-successional species grow and survive well in early-successional habitats if limitations to their dispersal can be overcome (Leopold *et al.* 2001; Hooper, Condit & Legendre 2002). However, if the lack of later-successional species in early-successional forest is due to physiological

issues that affect older seedlings and adult trees, such as low drought tolerance, then later-successional species will perform badly in restoration projects. Here, by considering specific functional traits rather than successional stage, these issues have been separated. However, by considering the coordination of functional traits into specific ecological strategies, the role of early-life traits as potential proxies for later life performance has been considered.

The aim of this study was to look at the functional traits of woody species found within the seasonally-dry tropical forests of northern Thailand to:

(a) Assess how species functional traits adhere to predictions under a variety of ecological models and to what extent this may provide information on the limiting factors and life-history strategies exhibited by woody species in the seasonally-dry tropical forest of northern Thailand.

(b) Predict the performance of species planted as part of a restoration project in Doi Suthep-Pui National Park using known ecological models, functional traits collected in the field and environmental data such as rainfall.

(c) Assess whether consideration of functional traits and performance can provide evidence for better species selection or restoration plot management in the future

Suitable functional traits were identified from previous studies and from ecological models such as the leaf economic spectrum. Trait data were collated from a variety of existing sources into a single database. Where existing traits were not available, they were collected from the field. These functional traits were then analysed in conjunction with performance data collated from the FORRU performance database.

9.3. Evaluation of project results

The following considers the results from this project in the context of its aims and objectives (see page 190)

9.3.1. Linking functional traits to ecological groupings

Predictions of groupings based on the leaf economic spectrum (Wright *et al.* 2004) have broadly been supported, with the suggestion that protection from herbivores acts as a separate axis. The importance of phenological leafing strategy (evergreen and deciduous) appears linked, not only through their differing positions within the leaf economic spectrum, but also to distinct differences between evergreen and deciduous species linked to drought tolerance requirements. The co-ordination of evergreen and deciduous characteristics, not only with leaf traits, but with wood traits has been of particular interest. Multiple axes of the wood economic spectrum (Chave *et al.* 2009) have also been supported. The differing patterns of growth for evergreen and deciduous species, and for recalcitrant and orthodox seeds has also proved useful and in line with predictions.

9.3.2. Predictions of performance using functional traits

Here, wood and leaf functional traits have been shown to be good predictors of growth rates, with wood traits being particularly useful. The models produced in Chapter 7 emphasise the importance of the different axes of wood variation (i.e. water storage, mechanical strength and hydraulic architecture) in predicting growth whilst emphasising the different patterns of growth for evergreen and deciduous species. Seed traits have also been found to be useful in predicting growth rates due to the co-ordination of seed and later traits as predicted by the CSR triangle.

Predictions of survival using functional traits have been less successful, but suggested that that there were a number of different limiting factors that affected survival in different environmental conditions in different years. In particular, the influence of pathogens and species resistance to pathogens has been inferred. However, without further work these remain hypotheses.

9.3.3. Evaluation of project success

The framework species approach suggests the selection of species based on a number of criteria. Of these criteria, the following were considered here;

Early and fleshy fruiting

The prediction of early fruiting from functional traits (maximum height, leaf tensile strength and phenological leafing strategy) or from nursery growth rates suggested that this approach could be very valuable and the relationships found fitted well with the concept of the ruderal or pioneer species. However, the small number of species available made modelling these results impossible. The approach of using functional traits is therefore supported, but this needs to be confirmed by future work. Both pioneers and ruderal species are predicted to have small dry fruits. It is predicted by both the pioneer/climax model and the CSR model that species cannot have both fleshy fruits and early fruiting. It is inherent to the framework species approach that pioneers are planted to provide shade and later-successional species to provide fleshy fruits. However, here, no evidence for a link between early fruiting and fruit fleshiness was found, suggesting that the separation of functions within the framework species approach may not be valid for northern Thailand. The small number of species for which data were available and the inevitable bias in this dataset due to the process of selection undertaken by FORRU do not allow any conclusions to be made. However, this is an intriguing area for future work which would have strong implications for species selection in the future.

Germination

Predicting reliable and fast germination using functional traits was very successful, with clear relationships between germination rates and both germination type and seed size. Phenology was also a useful indicator of MLD which should assist in producing nursery schedules. The use of a functional trait approach was therefore supported.

Survival and growth

Two of the most important criteria for framework species are that they will grow fast and survive well. The growth-survival trade-off would suggest that it is not possible for a species to possess both of these characteristics simultaneously. This clearly has implications for species selection and management in restoration projects. This could have resulted in recommendations to avoid planting species with very fast growth rates. Currently, an equal number of each tree species are planted. If evidence had been found for the growth-survival trade-off, it might have been valuable to adjust the number of trees of each species planted to encourage more equal representation of species after the first year. I.e. plant more of specie with fast growth in the nursery and fewer with slow growth.

Here, wood and leaf functional traits have been shown to be good predictors of growth in the field. The models produced in Chapter 7 emphasised the importance of the different axes of wood variation (i.e. water storage, mechanical strength and hydraulic architecture) and the different patterns of growth for evergreen and deciduous species in predicting growth. The project was successful in predicting growth using functional traits and the value of using functional traits to predict growth rates is strongly is therefore supported.

The prediction of nursery growth rates from functional traits was only successful for species with orthodox seeds. It is possible that the lack of such relationships in recalcitrant species may be addressed through the addition of other functional traits such as soil content. Therefore, the validity of the method appears sound.

It was not possible to link survival in all years with functional traits. Whilst there is evidence for specific functional traits linked to survival of different years, there was insufficient data to draw any conclusions. The strong suggestion of a role of pathogens and herbivores in survival has implications for both species selection and management regimes. I.e., the application of pesticides in specific years when there are higher numbers of herbivores. Whilst the use of the functional trait approach was not successful in predicting strong performance ere, it has suggested routes for further study.

9.4. Limitations of project

9.4.1. Implications of multiple significance testing for inflation of Type 1 errors

Here, a great number of correlations were performed. This increased the risk of a Type I error, (incorrect rejection of a true null hypthesis). Some of the measurements used here were derived from the other measurements (e.g. xylem diameter and xylem cross-sectional area), which further compounded the issue. Type I errors occur because statistical tests do not find absolute proof of a relationship but instead find the probability that the relationship identified could occur by chance. It is generally accepted that a less than 5% or 1% chance is significant enough. However, he more correlations that are performed, the more likely it is that one of these 1 or 5% chances could occur. Here, this risk was not adequately considered. This issue could be avoided in the future by;

- Using the bonferroni test to provide a new threshold of significance appropriate for the number of correlations performed
- Focus tests more carefully where there were strong valid reasons for predicting a relationship; therefore performing fewer correlations.

9.4.2. Implications and ecological interpretation of measuring leaf toughness based on estimating leaf tensile strength.

Here, leaf breaking point, a measure of leaf tensile strength was considered rather than the more usual measure of leaf toughness, the punch test (Choong *et al.* 1992; Read *et al.* 2009; Kitajima & Poorter 2010; Kitajima *et al.* 2012), which has a well supported relationship to leaf fracture toughness. Leaf fracture toughness has been linked to increasing leaf lifespan by protecting leaves from herbivore damage (Kitajima & Poorter 2010) and is therefore associate with the leaf economic spectrum. Leaf tensile strength was chosen over the punch test, primarily due to the low technology equipment that was required (Balsamo *et al.* 2004). However, tensile strength, which measures a tearing action is less likely than fracture toughness to accurately represent the feeding technique of herbivores. It would be valuable to calibrate the tensile strength test against both the punch test method and against actual levels of herbivore damage to assess the validity of this approach.

9.4.3. Implications of variable lengths of the first (5 month) and second (12 month) growing seasons for the comparisons of growth over time in Chapters 5 and 6

Growth and survival data were collected at the end of the wet season (November in each year); 5 months and 17 months respectively after planting in the field. Growth over the second season was therefore greater, merely because it was over a longer period. This had implications for which statistical tests and comparisons were possible. One solution to this may have been to calculate growth rates over each season separately. However;

- As well as its length , the quality of the period over which performance was measured also differed. Whilst measurements of growth and survival in the second year cover all seasons of that year, measurements of growth and survival in the first year were over approximately 2/3 of the wet season (seedlings were planted in late June, whereas the wet season usually starts in April) and did not include the dry season.
- Rainfall patterns and specifically the timing of the monsoon varied between years, so resulting in wet seasons of differing length in each year.
- Species differed in the number of months they had in leaf and the timing of their flush (in deciduous species) therefore altering the effective growing season for each species.

Due to these issues, comparison of growth in the two seasons would not have been appropriate. Therefore, instead of using growth rates to compare growth in the first season to that in the second season, comparisons were limited to interspecies differences. For example; the ratio of growth in the second season to that in the first was compared between species. If a future project were undertaken, it would be valuable to measure both and assess survival after both the wet and the dry seasons as this would help address this issue as well as providing valuable information on seasonality of seedling growth and mortality.

9.4.4. Implications of the collection of shade leaves for the measurement of leaf traits

Leaves can vary considerably, even within the same plant, due to phenotypic plasticity in response to light (Givnish 1988). This makes the comparison of leaf traits more complicated. It is therefore usual to collect traits from sun leaves when comparing species (Cornelissen *et al.* 2003). However, here, shade leaves were used. The reasons for this decision and implications for the interpretation of results are detailed below.

In order to reduce the effect of sapling age and phenotypic differences due to differing environmental conditions, all leaf samples were taken from saplings planted in restoration plots planted in 1998 and 1999. As sapling height varied considerably, some of the seedlings were part of the canopy and had both sun and shade leaves, whereas others existed only under the canopy and therefore possessed only shade leaves. Therefore, for comparison purposes, it was necessary to collect shade leaves for analysis. However, this may reduce the validity of some of the leaf traits collected as;

- The quality and amount of light that falls through a canopy can vary considerably, both in terms of intensity and quality and the extent to which leaves possess shade characteristics may therefore also differ significantly. However, as these traits were collected on the same plots, this impact should be reduced.
- The level and type of phenotypic plasticity in response to shade may vary between species. Recent findings suggest that responses to shade are mostly proportional, and therefore, rankings of species by shade or sun leaf will be very similar (Rozendaal, Hurtado & Poorter 2006). However, it would be valuable to confirm this within this particular habitat by comparing shade and sun leaves for a number of species to assess the extent to which specific leaf functional traits are correlated.

9.5. Suggested further work

9.5.1. Performance data

Here, performance data was used for 54 species and over four years of planting. Whilst later years' data were available, the restoration project run by FORRU undertook an ongoing process of identifying "bad" framework species, which were then not planted again and of improving field management technique through the continuing use of trials (Elliott *et al.* 2003). Also, the pre-selection of species that were most likely to be successful, based on early, unpublished trials and field observations, created an inevitable bias within the dataset. As comparisons based on performance, both between-species and between plots, were necessary here, later years' data were therefore not used, which resulted in a very small dataset.

This highlights the conflicting requirements of research and of successfully creating restored forest, especially where there are local needs for improved ecological function and where local support and funding reliant on the demonstrable value of projects for the local community. Whilst it might be necessary for research purposes to plant unsuccessful species, and to allow seedlings to die due to drought or disease, this is in direct conflict with the need to successfully create restored areas of forest. Additionally, phenotypic plasticity caused problems in separating potential growth rates and responses to limiting factors such as drought as "Competitor" species show significant levels of phenotypic plasticity (Wonkka *et al.* 2013).

If funding and space allow, it may be possible to demark different areas for research and for restoration purposes, to allow for these differing needs. However, this would create further strain on funding, and may, therefore , be impractical. Another approach may be to separate these two functions by pooling resources between projects to create a small number of research-based plots, whilst maintaining the community value of other areas.

9.5.2. Nursery performance and functional traits

The results of this study suggest that early performance in the nursery may be useful indicators of later performance. Additionally, ontological differences between early-life and later traits may be valuable. For example, through direct observation and discussions with FORRU staff, it became clear that many of the species considered here showed marked differences in leaf form, trichomes, leaf margins and bark lenticels between seedlings and adult plants. As the focus here in the nursery was on the production of healthy seedlings for the field trials (Blakesley *et al.* 2002; Elliott *et al.* 2002), management techniques were used to maximise survival and growth. However, seedling survival and growth in response to differing environmental pressures may provide useful information in predicting later performance as early indications here support a relationship between growth rates in the field and seed traits in line with previous findings (Moles & Westoby 2006; Wright *et al.* 2010). The undertaking of detailed nursery growth trials and the recording of morphological characteristics in early life may, therefore, allow better understanding of how early growth affects later performance. Information on survival and growth of seedlings in response to light drought and shade would also be useful as juvenile light requirements have been found to be related to later performance (Valladares & Niinemets 2008) .

9.5.3. Measures of performance in the field

The field trials undertaken by FORRU aimed to identify to species that performed the required roles rather than to identify species traits linked specific elements of performance, such as survival of the dry season, or level of phenotypic plasticity in response to differing environmental pressures. The performance measures collected here reflect that. The results here suggest that performance may be affected by both herbivores and drought, as identified in other seasonally-dry tropical forests, and that these factors vary between years. This could be confirmed through the collection of more detailed performance data, such as survival after both the dry and wet season and the level of herbivore damage observed at different stages.

It would also be useful to undertake trials linked specifically to pathogens, such as comparisons of plots with where differing anti-pathogen treatments have been applied.

Fruiting abundance data were not collected in a systematic way for most species. Fruiting abundance is an important characteristic of the Framework Species Approach (Goosem & Tucker 1995) and it would be valuable to have data on this. However, measurement of fruiting abundance is difficult and time-consuming and finding a practical approach may be difficult, especially in a field situation.

9.5.4. Functional trait data

This project relied on functional traits available from both literature sources and field measurements. Results have suggested some relationships that could have been further supported or rejected if additional trait information or alternative experiments had been performed. Whilst leaf, seed and wood characteristics were collected, root data was not. Given the importance of root characteristics in a water-limited environment such as the dry season in seasonally-dry tropical forest (Chaturvedi, Raghubanshi & Singh 2011), the predicted root characteristics of pioneer species (Pavlis & Jenik 2000) and the links between transplant shock and root traits , root data may be particularly useful in predictions of survival. It would be particularly valuable to collect data on root growth rate spread and depth as well as root-shoot ratio (Kitajima 1994). As part of considering the implication of differing levels of investment in leaves, shoots and total photosynthesising area as well; i.e. number of leaves rather than just the size and shape of individual leaves would be useful in assessing the allocation of resources. Leaf life-span is an important characteristic in the Leaf Economic Spectrum(Wright *et al.* 2004) and is discussed here, with the leafing period of deciduous species used as a proxy. However, it would be useful to extend this into evergreen species and provide measures of actual life-span measures in response to environmental factors.

9.5.5. Functional traits and links to performance

Many assumptions on the role of functional traits have been made here. Specific experimentation would be valuable to confirm the link of these traits to these roles functions within the study set. Specifically;

(a) The potential role of herbivores and fungi in shaping the protective features of leaves has been suggested. The anti-herbivore and pathogen role of calcium and tensile strength in leaves has been discussed. These hypotheses could be tested with controlled field experiments involving herbicides, fungicides and direct observation of pathogen and herbivore load.
(b) The role of wood characteristics in preventing cavitation have also been inferred from other studies (Chave *et al.* 2009). Direct measurement of hydraulic capacity and cavitation would be useful in confirming these relationships.
(c) The relationship between herbivore resistance and leaf tensile strength and between leaf tensile strength and leaf punch strength could be tested as a method of calibrating results here against more traditional measures.

9.6. Conclusions

This project has confirmed relationships between a number of desirable traits for forest restoration using the Framework Species Approach (FSA) and easily measured functional traits within the seasonally-dry tropical forests of northern Thailand shown the value of using functional traits in selecting species for restoration projects in some but not all of the selection criteria for framework species. Specfically, it was been found to be valuable in selecting species based on growth rates, germination success and

However, where it has not been successful in identfying criteria using functional traits, (such as in the area of survival) , itt has suggested other avenues of further research and specifically raised resistance to pathogen and herbivore damage as a useful area for further investigation.

The project here was based in evergreen hill forest. Seasonally-dry tropical forest often experiences far longer and more intense dry seasons than this particular forest type (Murphy & Lugo 1986) and projects in other areas may find that drought is a larger driver than has been found here and pathogen and herbivore damage a lesser driver. Further work in other areas to establish these axes of variation may be helpful.

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